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Consequences of Insular Population Structure: Distribution and Extinction of Spruce Grouse Populations in the Adirondack Mountains

Robert S. Fritz

Introduction

Islands are precisely defined patches of habitat. The theory of island biogeography (MacArthur & Wilson, 1967) predicts that the number of species on an island reaches an equilibrium due to the opposing forces of immigration and extinction. Rates of immigration are related to the distance of the island from a source of colonists, and extinction rates are related to the area of the island, a rough indicator of the variety of habitats available for colonization. Evidence supporting these predictions is reviewed by Simberloff (1974).

The heterogeneity of habitats on a mainland suggests an insular arrangement of habitat patches; thus, principles of island biogeography should be applicable to mainland "islands". Studies of mountaintops, caves, and lakes have given support to this application (Culver, 1970; Johnson, 1975; Keddy, 1976; Vuilleumier, 1970). Individual plants can also be considered ecological islands (Janzen, 1968; Opler, 1974; Siefert, 1975).

The subset of available species found in habitat patches are those able to colonize and persist in the patches. Each species differs in its response to the patchiness of the habitat through its requirements of patch area and ability to disperse among the constellation of patches. Wiens (1976) discusses a number of populational responses to patchy habitats which can influence the presence of a species in a patch.

If the insular nature of habitat patches is important to the distribution of the species, then patch area and inter-patch distance should be important. The insular population structure of pikas *(Ochotona princeps)* shows an influence of patch size and inter-patch distance on local distribution (Smith, 1974).

I have studied the distribution of the Spruce Grouse *Canachites canadensis* in the Adirondack Mountains of New York State. Population densities in several patches were determined and are compared to populations in other regions. The influence of patch area and inter-patch distance was investigated in relation to the presence or absence of Spruce Grouse from suitable patches of habitat.

Methods

Habitats occupied by Spruce Grouse were located by verifying reported sightings from local residents and from the literature. Initially patches of coniferous forest consisting of black spruce *(Picea mariana)*, larch *(Larix laricina)*, balsam fir *(Abies balsamea)*, red spruce *(Picea rubens)*, or white pine *(Pinus strobus)* were field checked, whether they were in wet lowland areas or dry upland areas. In addition to known sites, potential locations of coniferous forest were determined from aerial photographs

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and LANDSAT satellite photographs. Data obtained from LANDSAT were multispectral images of the Adirondack Mountain region computer-interpreted and coded with symbols scaled to 7.5 minute U.S.G.S. topographic maps (ESCHNER et al., 1977).

To field check reported and potential locations one to three people walked through the habitat playing recorded vocalizations of female Spruce Grouse. During spring (April and May), and to a lesser extent summer (June—August) female aggressive vocalizations elicit from male Spruce Grouse a flight display audible from about 100 m. Males frequently approach the source of the sound. Females respond to the calls for a limited period by returning the calls and slowly approaching. Spruce Grouse could always be approached within one to three meters, so that all contacts were positive sightings. By moving throughout the site, nearly all the males and a lower proportion of the females could be located in repeated visits.

Scats of Spruce Grouse could be distinguished in the field from those of any other bird, including Ruffed Grouse *Bonasa umbellus,* by their shape, colour and texture. Scats were obvious where Spruce Grouse were found, even when birds could not be contacted with the taped calls.

Spruce Grouse were considered to constitute a distinct population when individuals were found in a patch of habitat separated from other suitable habitat by deciduous forest. This definition makes no assumptions about gene flow among populations. The presence of a population of Spruce Grouse was considered verified when males, females, or chicks were found; where fresh scats were found; or where Spruce Grouse had been reported by a person familiar with the grouse. Females were always more dif-

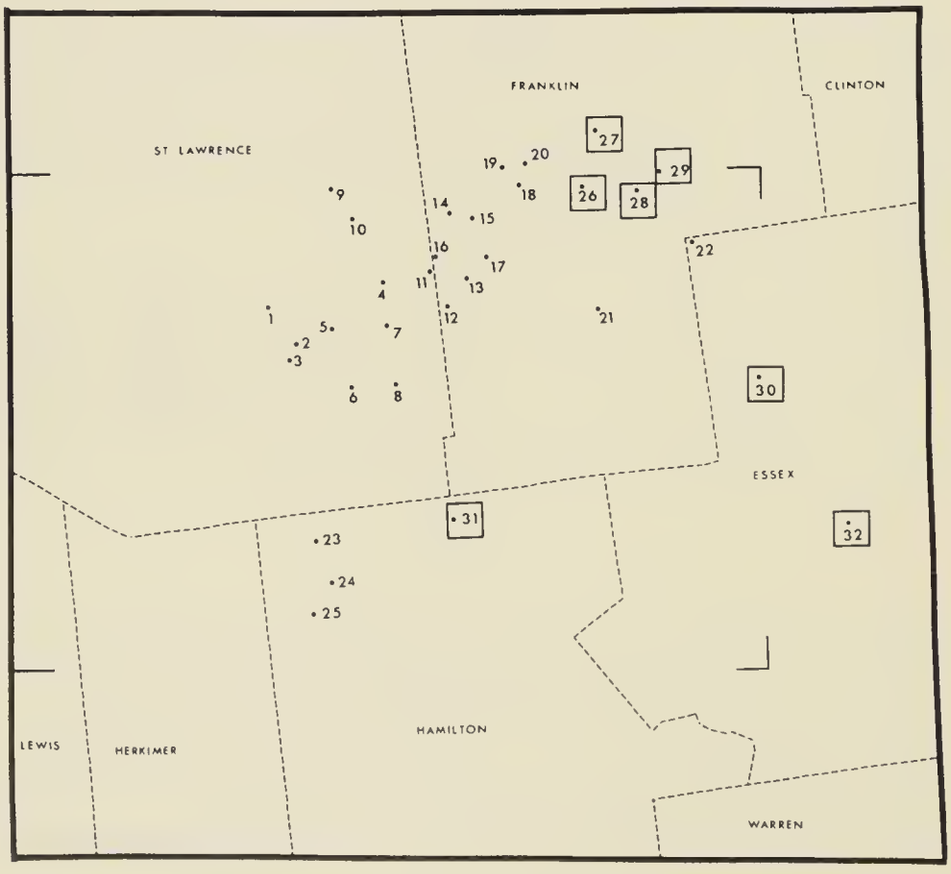

FIGURE 1: Locations of patches occupied in 1977 (1—25), and patches unoccupied in 1977 (26—32). Corners show the extent of LANDSAT coverage.

ficult to find than males, even when they were known to be present. Most of the sites were verified by the presence of females and males, with all but two being verified by the other criteria. These two sites had been known to have Spruce Grouse for numbers of years and had been verified during my study period by reports.

Other patches of habitat visited appeared in all ways suitable for Spruce Grouse, yet none were found. These patches were considered suitable but unoccupied if there had been previous reports of Spruce Grouse seen in these areas, or if they were very similar to occupied habitats.

Results

Occupied patches

During the study 220 field visits were made to 67 potential habitat patches, including coniferous forest found in the Adirondack Mountains, from black spruce-larch forest to subalpine balsam fir-red spruce forest. In 1977, 25 habitat patches were known to have extant populations of Spruce Grouse (Fig. 1).

Spruce Grouse occupied only black spruce-larch forests and thus, only a small proportion of the coniferous forest types available. Habitat selection studies of Spruce Grouse are consistent with this pattern (Haas, 1974; Robinson, 1969). That the Spruce Grouse utilize a narrow range of the available habitats is further supported by the narrow diet of adult Spruce Grouse, which consists of conifer needles and leaves and berries of associated herbaceous plants (Crichton, 1963; Ellison, 1966; Jonkel & Greer, 1963; Pendergast & Boag, 1970; Robinson, 1969).

Regional distribution of habitat

The distribution of lowland black spruce-larch forest can be compared between quadrangles with and without Spruce Grouse populations. Amounts of lowland coniferous forest were determined from LANDSAT coverage of Spruce Grouse range, except for two sites (Figure 1). Lowland coniferous forest is found in all patches having Spruce Grouse and is often the predominant vegetation. The validity of the computer-determined classification of lowland conifer, determined from comparisons to aerial photographs, was found to be 93 % accurate by Eschner et al. (1977). A comparison between quadrangles having and not having Spruce Grouse showed significantly more lowland coniferous forest in those quadrangles having Spruce Grouse (Mann-Whitney U test, $P < 0.0001$).

The number of populations, a rough measure of the abundance of Spruce Grouse in a quadrangle, can be related to the abundance of lowland conifer (log transformed) in the quadrangle ($r = 0.68$, $P < .01$).

Area, inter-patch distance, and population density

The mean size of the 25 occupied patches is 157 ha (Table 1), and variability in patch size is large. Ten of the largest patches occur in four adjacent quadrangles in the northern part of the range and contain 64 % of the total area of occupied habitat. The smallest patch (20 ha) inhabited by Spruce Grouse contained a pair of Spruce Grouse in 1976, but had no breeding population in 1977.

TABLE 1: Mean, standard error, and range of area and distance to the first and second occupied patches from occupied patches and unoccupied patches.

	Area (ha)	Distance (km) 1st	2nd
Occupied Patches			
Mean	157	5.2	8.0
SE	25	0.8	1.0
Range	28—591	1.7—17.2	3.0—24.4
Unoccupied Patches			
Mean	56	16.0	21.4
SE	11	3.4	4.4
Range	20—118	7.8—33.0	8.0—45.0

The mean distance to the nearest occupied patch is 5.2 km, while the mean distance to the second nearest occupied patch is 8.0 km (Table 1). If a population went extinct these distances represent a minimum distance that dispersing Spruce Grouse must travel to colonize the vacant patch. Patch area and inter-patch distance are not significantly correlated (Spearman Rank Correlation, $r_s = -0.285$, $P > .05$).

TABLE 2: Density of Spruce Grouse populations in patches where population sizes were known during 1977.

Patch	Area (ha)	Number of Spruce Grouse*	Density (Spruce Grouse/ 100 ha)
Sevey Bog	50	5	6.8
Grasse River	182	13 (1976)	7.1
		16	8.8
Hedgehog Club	88	4	4.5
Dead Creek II	114	4	3.5
Joe Indian Pond	33	2	6.1
Kildare Pond	37	2	5.4
Bloomingdale Bog	45	2	4.4
Mean			5.6

* Population size for 1977 unless otherwise indicated.

Numbers of Spruce Grouse were known reliably enough in 7 patches to estimate minimal population densities. The population sizes in each patch were determined from the cumulative number of marked birds found in a patch for 2 to 20 repeated visits through the spring and summer. The mean density for these patches was 5.6 Spruce Grouse/km^2 (Table 2). This range is an agreement with densities found in Michigan (W. L. ROBINSON, pers. comm.) and Alberta (MCCOURT, 1969; MCLACHLIN, 1970).

Unoccupied patches

Seven unoccupied patches were found that appeared to be identical to the occupied patches. The tree species were the same and in similar abundances, with identical asso-

ciated shrub and ground vegetation. Canopy cover and height in each appeared to be within the range observed in occupied patches. Spruce Grouse were known to have inhabited four of the patches, while three of the patches had less reliable reports of Spruce Grouse being seen there previously. Thus, it is reasonable to assume that the patches constitute suitable habitat. These patches lie at the periphery of the range (Fig. 1). The mean area of these patches is 56 ha, the mean distance to the first nearest occupied patch is 16.0 km and the mean distance to the second nearest occupied patch is 21.4 km (Table 1). Unoccupied patches are significantly smaller than occupied patches (Mann-Whitney U test, P = .012) but fall within the size range of the areas known to sustain populations of Spruce Grouse (Fig. 2).

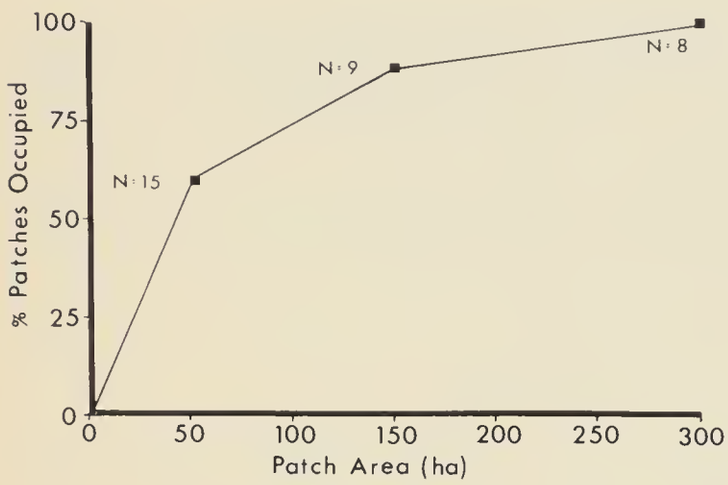

FIGURE 2. The proportion of patches occupied within a size class (100 ha).

Unoccupied patches were also significantly farther from occupied patches than were occupied patches from each other, P = .0003 (Mann-Whitney U test) for the first nearest neighbour and P = .0014 for the second nearest neighbour (Fig. 3). Because of the higher levels of significance in the distance relationship, distance may be a more important factor determining the presence or absence of a population than area, but clearly both factors are influencing the observed situation.

These data suggest that small patches far from a colonizing source should not be occupied. However two small, isolated sites are currently occupied. The similar Bog Stream site was occupied in 1976, but had become extinct in 1977. Bloomingdale Bog did not have Spruce Grouse in 1976, but a breeding pair was found in 1977. In addi-

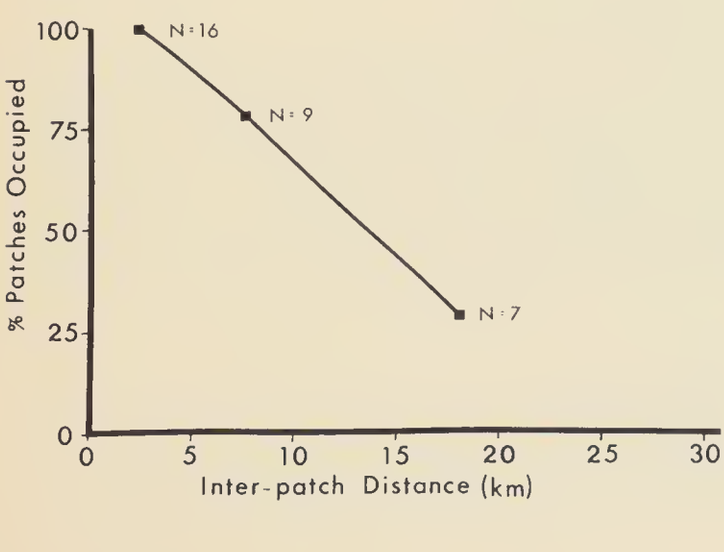

FIGURE 3. The percentage of patches occupied at different distances from the nearest occupied patch.

tion, a large patch close to an adjacent occupied site had no Spruce Grouse in 1976, but was again occupied in 1977. Two other sites which are far from a colonizing source have only one pair of Spruce Grouse and thus may be very susceptible to extinction.

Discussion

At the southern boundary of their range, the Adirondack Mountains, Spruce Grouse are restricted to insular patches of suitable habitat, and are separated from other populations of Spruce Grouse in Ontario by at least 200 km. Within the region the presence of Spruce Grouse is related to the abundance of lowland coniferous forest. The size of many habitat patches is small, with consequent small populations that are prone to periodic extinction.

Suitable unoccupied patches were significantly smaller and significantly farther from a source of colonists than occupied sites. These data suggest that dispersal is insufficient to maintain populations within a patch when population sizes are so small that frequent extinctions occur.

Smith (1974) found that as distance between patches increased the proportion of patches occupied by pikas decreased. As patch size increased, the percent saturation increased linearly, indicating dependence on population size in maintaining stable populations. When population size was small, dispersal was an important factor in maintaining the population because extinction rates were high.

Patch size and inter-patch distance can thus set the limits of a species' range even if habitat exists beyond the border. Changes in the reproductive success and dispersal frequency of a species may cause its range to fluctuate over time. Smith (1974) suggests that these effects probably influence the distribution of the pikas in California. These patterns are in general agreement with predictions of the influence of dispersal on crowding in discrete populations by Gadgil (1971). He has shown that if the likelihood of dispersing individuals reaching a particular habitat is not equal for all the patches because of greater isolation, they will tend to become less saturated. This will lower the density in patches and thus increase the probability of extinction.

The distribution of the Spruce Grouse in the Adirondack Mountains is related to the size of the populations and distance between them, which suggests that extinction and recolonization may be important factors influencing their stability over time.

Acknowledgements

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Turnover Dynamics in a Tropical Continental Avifauna

James R. Karr

Introduction

According to conventional ecological wisdom, biological communities of continental areas in the wet lowland tropics are stable; that is, species composition and relative abundances are about the same in any location from year to year. On the other hand, island situations exhibit considerable turnover of species and individuals (Jones & Diamond, 1976). Islands, it is reasoned, have low population densities and slow immigration rates, and therefore random events play a significant role in extinction and recolonization patterns. Many species in tropical mainland forest are present at low densities (Karr, 1977) predisposing them for higher turnover rates. Because weather varies from year to year, as does forest structure (tree species composition and/or vertical profile), these low densities should make tropical communities especially fragile. In this paper I show that both species and individual (changes in density of a species) turnover are regular in a tropical forest avifauna.

Study region and methods

A 2 hectare plot of seasonally humid forest ("Limbo Hunt Club") in the Pipeline Road area of the Panama Canal Zone has been the subject of detailed studies since 1968 (Karr, 1971, 1976a, 1976b). This forest receives about 2600 mm of rain per year, primarily in a rainy season lasting from late April to mid-December.

Detailed mist-net and observational samples are available for this intensive study plot for both wet and dry season in 1968—69 and for the dry seasons of 1975, 1977, and 1978. Typically, 11 to 15 mist-nets are deployed in a loop to cover an area of approximately 2 ha. Twelve-meter nets with 30 or 36 mm mesh are placed so that the lowest shelf makes contact with the ground for most of its length. In addition to use of mist-nets, I record all species seen or heard on the study plot during each visit.

Species densities and guild structure

Operation of mist-nets in the undergrowth of the tropical forest results in repeatable accumulation of species. Typically, 32 to 37 species are represented in the first 100 captures from wet forest in Central Panama in contrast to lower accumulation rates from forest in Africa and Southeast Asia (Karr, in prep.; Dowsett, this symp.). Even within the same forest in Panama, however, there is some variation in the number of species captured. During a full year of detailed study in 1968—69 a similar number of species (31, 32) were caught in both wet and dry season samples (100 captures). However, when a series of dry season samples are compared, variation seems to be correlated with the severity of the dry season. Two unusually dry years (1975, 1977) produced the highest number of species (34, 36) while two normal to wet dry seasons (1969, 1978) yielded lower numbers of species (30, 31). (A total of 57 permanent resident species

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TABLE 1: Number of species and individuals for each of 10 guilds in mist-net samples during 4 dry seasons

	Number of Species						Number of Individuals				
	Total*	1969	1975	1977	1978	CV	1969	1975	1977	1978	CV
Frugivore — (Terrestrial)	3	1	2	2	1	38.5	2	2	3	3	23.1
Frugivore — (Arboreal)	4 (2)	4	4	4	4	0.0	33	26	36	38	15.8
Insectivore-Frugivore — (Arboreal)	4 (1)	3	2	1	2	40.8	9	5	3	5	45.8
Insectivore-Nectarivore	6	1	3	4	3	45.7	4	7	11	8	38.5
Insectivore — (Bark)	4	2	2	3	4	34.8	6	3	3	6	38.5
Insectivore — (Terrestrial)	6 (2)	4	5	6	5	16.3	9	8	11	8	15.7
Insectivore — (Foliage)	15	9	10	8	5	26.6	18	21	20	16	11.8
Insectivore — (Sallier)	3 (1)	3	4	2	2	34.8	7	12	4	7	44.2
Insectivore — (Ant-follower)	5	3	3	4	3	15.4	11	15	9	8	28.8
Misc. (Raptors, piscivores, etc.)	3	1	1	0	1	66.7	1	1	0	1	66.7
Totals	39 (6)	31	36	34	30	32.6	100	100	100	100	32.9

* Total all dry season samples — Residents (Migrants)

and 6 migrants which breed in the North Temperate Zone were captured in the four dry seasons.)

Two factors may be responsible for the high number of species in the dry years. First, there is often an influx of birds from drier Pacific coast habitats during especially dry years (Karr, 1977). Second, some species may shift foraging activities to lower levels in the forest during dry periods, a seasonal analogue of the diurnal shifts observed in foraging antbirds (Pearson, 1971).

In addition to the constancy in species number the trophic structure of the communities remains relatively constant; that is, the number of species and the number of individuals in each of a series of food resource guilds is relatively stable (Table 1). However, certain guilds are more variable than others. Arboreal fruit-eaters vary little in number of species (CV-0) and individuals (CV-16) among the years while insectivore-nectarivores are highly variable (species CV-46; individuals CV-39), as are insectivore-frugivores (CV-41 and 46). Although there is a significant correlation ($r = .801$, $p < .05$) between the variability in number of species and individuals, not all guilds follow the general rule. The number of ant-following species, for example, is relatively constant (CV-15) while the number of ant-following individuals varies more among years (CV-29). Low variation in number of species probably reflects the general distribution of ant-following species throughout the region (Willis, 1967). More importantly, their varying local abundance is likely due to variation in local distribution and abundance of ant swarms. For an unknown reason the most abundant ant follower during the 1969—77 period *(Hylophylax naevioides)* was not seen or captured during the standard sample in 1978 at Limbo Hunt Club.

The number of species of foliage-feeding insectivores remained relatively constant for the first 3 dry season samples (8—10; CV-13) but dropped strikingly in 1978 to 5 species (4 sample CV-27). The reason for this shift is not clear. Note that some form of density compensation may exist here; the number of individuals captured declined by only 20 % but the number of species declined by 60 % from the previous sample. The most variable major guild (ignoring "Misc.") is the insectivore-nectarivores which varies from 1 to 5 species in 100 captures (CV-46). The number of insectivore-nectarivores seems to peak in dry years with an influx of species from drier regions.

In addition, change in species composition among years varies among guilds. For terrestrial insectivores a total of 8 species were captured but only 1 was captured in all 4 years, 4 were taken in 3 years (3 of 4 in consecutive samples), 2 were captured in 2 years and only 1 in one year. The leafscraper *(Sclerurus guatemalensis)* is the only species caught in all 4 years. In one case, a species *(Myrmeciza exsul)* was not captured in a year of netting but has been present in recent (1975—78) samples. At the same time, a species with similar feeding ecology *(Formicarius analis)* captured in early samples was not represented in 1978. The replacement of *Formicarius* by *Myrmeciza* seems to be a result of habitat changes associated with treefalls.

In some guilds, species regularity was high but abundances changed from year to year. Undergrowth frugivores were represented by 4 resident species in the 4 dry season samples and three of these were taken in all 4 years. The other species *(Manacus vitellinus)* is represented in only one year, as an accidental from more suitable habitat nearby. The 3 species taken in all years varied in abundance from year to year (Table

2). The most abundant species *(Pipra mentalis)* has the most variable capture rate while the fruit-eating tyrannid *(Pipromorpha)* was least variable in abundance and capture rate.

The only other guild with a majority of species caught in all years was the sally-feeding insectivores. Two of three permanent resident species in the guild *(Terenotriccus erythrurus* and *Onychorhynchus mexicanus)* have quite variable densities (CV-34.8 and 80.9, respectively). All other guilds except foliage insectivores have only one species caught in all four years. Among the foliage insectivores only *Myrmotherula fulviventris* (an antwren) and *Platyrinchus coronatus* (a tyrannid) were caught in all years.

TABLE 2: Number of captures and capture rates (birds per net hour) for undergrowth frugivores in 4 dry seasons

		1969	1975	1977	1978	coefficient of variation
Pipra coronata	numb. capts.	10	4	6	6	38.7
(Blue-crowned Manakin)	capture rate	0.026	0.013	0.023	0.016	30.9
Pipra mentalis	numb. capts.	11	10	20	21	37.4
(Red-capped Manakin)	capture rate	0.028	0.033	0.078	0.055	47.2
Pipromorpha oleaginea	numb. capts.	9	8	9	10	9.1
(Ochre-bellied Flycatcher)	capture rate	0.023	0.026	0.035	0.026	18.9

In general, migrant species were very sporadic in their occurrence. Out of the 6 migrants, three were caught in only one or two years. Residents, on the other hand, were caught in all possible sequences with most being caught in only one year (19 species) and 13 being caught in all 4 years. The distribution of species among the groups (number of years captured) is, however, not significantly different from random ($\chi^2 = 3.68$ — residents only; $\chi^2 = 5.34$ — residents and migrants combined).

When all species recorded on the study plot are considered, a total of 161 species were recorded in the four dry season sample periods: 1969—99; 1975—82; 1977—105; 1978—95. Most (55) were recorded in only one year while many (43) were recorded in all four years. The distribution among the 4 groups is significantly different from random ($\chi^2 = 9.7$, $p < 0.05$).

Differences among samples

An early objective of this research was the determination of turnover rates in a continental forest bird fauna. I shall use the following indices to measure differences (turnover) between samples:

$$PD_s = \frac{100\,(a' + b')}{a' + b' + c'}$$

$$PD_a = \frac{100\,\Sigma|\chi i - \gamma i|}{X + Y}$$

where PD_s = percent difference by species only,
PD_a = percent difference by species and abundance,

a′ and b′ = number of species in samples A and B only, respectively,
c′ = number of species in both samples A and B,
X and Y = number of individuals in samples A and B respectively,
χi and γi = number of individuals of species i in samples A and B, respectively.

Because two simultaneous samples could not be entirely different it is necessary to determine a minimum difference between two subsamples of a single large sample. The largest sample collected in a few days contained 172 individuals and was divided by allocating odd-numbered and even-numbered captures to separate subsamples. PD_s is 38 and PD_a is 36 (86 capture samples; Table 3). Note that PD_s and PD_a are essentially the same value. Since percent difference declines slightly as sample size increases, I shall assume a value of 35 for 100 bird samples. All subsequent comparisons will be made using this index as a minimum (baseline) difference.

When wet and dry season samples are compared within the 1968—69 study period PD_s is essentially the same as the baseline index of 35. PD_a is larger than the baseline suggesting that, in contrast to within-sample differences, there is more variation in abundances than in species composition.

TABLE 3: Percent difference in the composition of mist-net samples from Limbo Hunt Club

Season	year	N	percent difference species only	percent difference species and abundance
Wet (Subsamples)	1976	1	38	36
Wet vs. Dry	1968 vs. 1969	1	34	48
Dry	1968, 75, 77	3	52.3 ± 3.8	58.7 ± 2.1
	1968, 75, 77, 78	6	55.7 ± 4.8	56.8 ± 6.7
Wet vs. dry (diff. years)	1968 vs. 1975, 77, 78	3	57.0 ± 7.2	65.3 ± 3.2

PD_s and PD_a calculated using data from three dry season samples (1969, 1975, 1977) are well above baseline differences (Table 3). Pairwise comparisons including data for 1978 yielded about the same mean as found in the first three years of data but somewhat higher variability. The significance of this pattern becomes clear when one considers the weather situation during each of the sample periods. Both 1975 and 1977 were exceptionally dry during the dry season while 1969 was more near normal. The dry season of 1977 was unusually dry; during two weeks of field work at Limbo Hunt Club in 1977 the only rain was very light and lasted for less than 2 minutes on one day. In contrast, during two weeks in 1978 it rained every day and included at least two days of extended rain lasting in excess of several hours. The increased variability resulting from the addition of 1978 data seems to be due to the wetter conditions during that year. PD_s among the first 3 dry season samples was low (52.3) while PD_s for 1978 compared to the other 3 years was higher at 59.0.

Finally, the differences in the samples are greatest when dry season samples are compared with wet season samples from another year (Table 3).

At this point a major question might be raised about the adequacy of 100 bird samples for detecting year-to-year variation in community structure. When the more com-

plete lists of all birds seen or heard on each visit are compared PD_s equals 50.6 ± 4.3. This is somewhat smaller but not significantly different from mist-net samples for the same comparison (55.7 ± 4.8, Table 3). As with the mist-net samples differences among dry season samples in 1968 through 1977 are lower (47.7 ± 3.8) than are those samples from 1978 (53.4 ± 2.6) although the means are not significantly different. Since relative abundance data are not available PD_a cannot be calculated. The similarity of PD_s for mist-net and all species samples supports inferences from mist-net studies.

Conclusion

Clearly, the avifaunas of tropical forest are not constant as both species composition and relative abundances change over short time periods. Changes seem due to changing weather conditions (e.g. among dry seasons) and to changing composition and structure of vegetation. Variation (turnover) differs among guilds in a distinctly nonrandom fashion indicating that major ecological correlates of turnover should be sought. Species composition changes regularly in some guilds (ground-feeding insectivores), abundances in other guilds (undergrowth fruit-eaters, ant-followers), and both composition and abundances shift markedly in others (nectarivore-insectivores). "Random" variation may also be of some significance in guilds where species tend to be present in low densities. Differences between seasons in the same year tend to be lower than differences among years at the same season.

Acknowledgement

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Dynamics of North European Bird Communities

Olli Järvinen

Introduction

In a travel report describing South America, the Finnish author Olavi Paavolainen contrasted oceanic islands with continents. He observed that islands are like poems: they are small worlds, which are possible to survey completely, but continents resemble epics. I feel this contrast also applies to the study of community dynamics. The dynamic theory of island communities is like a brilliant and crystallized poem, but the study of continental dynamics has produced many different patterns, which are difficult to integrate with each other.

In the following, I shall review dynamic patterns in bird communities in the light of North European studies. My examples have a broad spatial and temporal range, from a few hectares to half of Europe and from successive breeding seasons to studies covering many decades. The study areas include true islands, habitat islands, and wide areas of the continent, but the patterns to be studied are in each case essentially continental. Without exception, I shall be concerned with breeding birds.

My use of "species turnover" is identical with the standard in island studies (e.g. Diamond, 1969), but I shall also discuss density changes in communities ("individual turnover" might be a proper term).

Birdsong valley: A model community

Birdsong Valley is a rich deciduous forest of 13 ha in southernmost Sweden. The community supports slightly over 100 pairs of small passerines each breeding season. Birdsong Valley was surveyed by Anders Enemar (1966) in 1953—62, and I shall choose this careful study as my starting point. The following patterns emerge (Enemar, 1966; Järvinen & Väisänen, 1976; Järvinen, unpublished):

1) Small passerine numbers varied little, the coefficient of variation of density being 5.4 % in the ten-year period.

2) The average population fluctuated more than the total community (measured with coefficient of variation); in other words, the population changes were partly compensatory.

3) Species turnover was about 10 % per year, and the number of species was apparently at equilibrium. The turnover was mainly due to immigration and disappearance of species present at low densities (1—2 pairs).

As Birdsong Valley is productive by North European standards, the relative stability of the community may well be due to high productivity, as suggested by Enemar (1966): Birdsong Valley is optimal for many species, and it is thus each season fully packed with birds, even if general population levels show considerable fluctuation. The community may thus be unrepresentative.

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Geographical gradients of community stability

The generality of the patterns observed at Birdsong Valley can be examined on the basis of community studies made in other areas. A detailed analysis of about 15 5-to-10-year censuses, covering the northern half of Europe, suggests (JÄRVINEN, unpublished) that Birdsong Valley is characteristic of Central European and South Scandinavian communities, but not of northern Scandinavian ones. Total density typically varies three times as much in the north as at Birdsong Valley (comparison based on coefficients of variation), and species turnover is often more than 15 % per year, in contrast to the 10 % or less in more southern communities. The transition from relative stability to relative instability seems to occur within the boreal (coniferous) zone.

The geographical pattern observed thus supports the classic ecological dogma that northern communities are less stable than southern ones, but this dogma has been questioned in recent years on the basis of empirical and theoretical arguments (see e.g. GOODMAN, 1975).

The northward decrease of community stability can hardly be interpreted satisfactorily on the basis of the productivity hypothesis suggested for Birdsong Valley. Many northern communities are occupied by northern species always breeding in the north, whether southern habitats are saturated with birds or not. Environmental productivity may thus explain stability differences within the same geographical area, but major trends require other explanations. My guess is that the main factor is unpredictability: the breeding season of the north is not only brief, but also often interrupted by occasional snowstorms or other kinds of adverse weather. Exact quantitative measurements of annual fluctuations of bird communities should certainly be made in southern Europe and Africa in order to find whether the gradient found in the northern half of Europe is globally valid.

I suggested that community stability clearly decreases within the coniferous zone in Europe. Swedish bird census data (mapping censuses 1969—71; SVENSSON, 1972) are an important source here. I have here included the forest censuses (n = 28), but averaged the data for all plots representing the same habitat in the same area, so 21 observations were available. Most study plots were 10 ha or slightly more (range 8—40 ha).

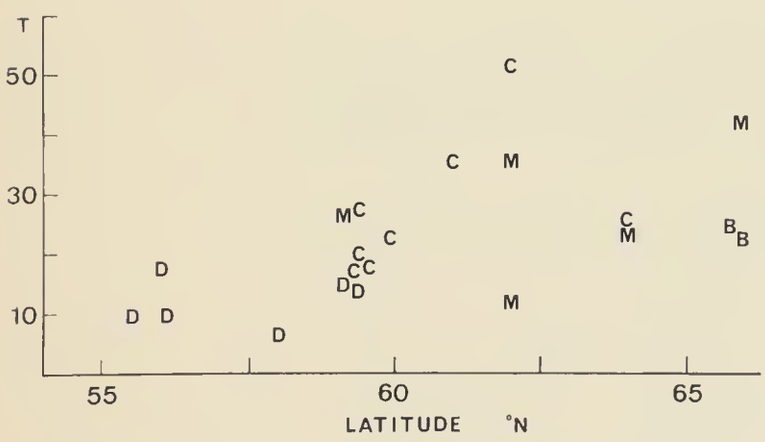

FIGURE 1. Relationship between species turnover (T, in %) and latitude in 21 Swedish bird census areas. All habitats are forests: B = mountain birch, C = coniferous, D = deciduous, M = mixed deciduous-coniferous.

Species turnover estimates (JÄRVINEN, unpublished; Fig. 1) suggest that species-rich and dense communities in the south show less turnover than species-poor low-density communities in the north. I interpret the clear trend seen in Fig. 1 as a result of greater unpredictability of the northern environments, though it is difficult to make a distinc-

tion between the effects of environmental predictability and, say, diversity, on community stability, as diversity also decreases northwards (for data, see JÄRVINEN & VÄISÄNEN, 1973, 1978 a).

Environmental unpredictability is not, however, the whole truth, or if it is, it is only indirectly so. Turnover in this material is mostly due to one-pair populations; they account for about 70 % of all disappearances. A simple explanation for the trend in Fig. 1 would thus be that northern and southern communities have different species-abundance relations. This is, indeed, correct, for the dense, species-rich southern communities contain proportionately fewer very small populations (one pair per species). But this correlation is not strong enough to account for the whole trend. The northern populations are thus, on average, highly vulnerable because of their small size, but they also live in an environment with great hazards. Fig. 1 suggests that habitat differences are a major cause, but this is probably a secondary phenomenon, as different habitats are dominating at different latitudes. My unpublished data suggest that geographical location is of greater importance in determining community stability than habitat.

The studies reviewed thus far were based on census periods of 10 years or less. I shall now take a longer perspective, for many new patterns will emerge.

Long-term trends of the Finnish avifauna

Ornithologists have been active in Finland for more than 100 years, though the number of ornithologists has increased explosively. It is thus possible to study the changes in the list of regular breeders in Finland during the 19th and 20th centuries. I was not able to find any species which certainly bred regularly in Finland in the early decades of the 19th century, but then disappeared. This must, however, be an underestimate, because small regular populations of certain species may have been overlooked by the 19th-century ornithologists. So I guess that the rate of disappearance has been one species per many decades. The fauna has not been at equilibrium, for 25 new species is a minimum estimate, implying about two new species per decade. These rates are incompatible with the hypothesis that North Europe is being gradually reinvaded after the last Ice Age; the recent trend must have more immediate, and more ecological explanations.

The dynamics of a fauna not only consist of changes in the species list, but also of changes in the ranges and densities of species. Three different estimates are available (Table 1). VON HAARTMAN (1973) summarized mostly qualitative data; JÄRVINEN &

TABLE 1: Population Trends of Finnish Birds in Recent Times

Species Group	Period	Trend** +	±	—	Source*
All Finnish species (233)	c. 100 yrs	34 %	42 %	25 %	(1)
86 most abundant land birds	30 yrs	43 %	28 %	29 %	(2)
40 most abundant forest species	50 yrs	72 %	18 %	10 %	(3)

* Sources: 1 = VON HAARTMAN (1973), 2 = JÄRVINEN & VÄISÄNEN (1977), 3 = JÄRVINEN & VÄISÄNEN (1978 b).

** Symbols of trends: + increasing, ± stable or fluctuating, — decreasing.

Väisänen studied (1977 a), using quantitative census data throughout Finland, population trends in the abundant Finnish land birds; and Järvinen & Väisänen (1978 b) made a quantitative study of the abundant south Finnish forest species.

The result is clear: many more species have increased than decreased in Finland in recent decades. There are various possible interpretations. An important early hypothesis was that climatic amelioration explains why most of the increasing species are southern, and most of the decreasing species are northern (e.g. Kalela, 1949). As climatic amelioration has not continued in Finland in recent decades, it has become possible to test the climate hypothesis, and it seems that climate is not a major factor in explaining the population changes observed (von Haartman, 1973). Man seems to be a far more important agent in explaining the recent trends in the Finnish avifauna:

1) The forest area has greatly increased due to drainage of peat bogs and afforestation of agricultural areas (Järvinen et al., 1977);

2) The bush layer of the forests has become denser due to the abandoning of forest grazing by cattle (von Haartman, 1973) and artificial fertilizers applied in forestry (Järvinen et al., 1977);

3) The extent of young developmental stages and forest edges have increased due to forestry (Järvinen et al., 1977);

4) Lakes and coastal bays have been eutrophicated, and grazing pressure on shores has decreased (von Haartman, 1973, 1975).

In Sweden, Ahlén (1975 and earlier) has also stressed the effect of man on bird population trends. In fairness to Kalela, I stress that he observed most of the above trends (Kalela, 1938), though he emphasized climate.

It may be questioned why southern species have increased more often than northern ones, if most range expansions are due to man. The reason seems simple: if a southern species is capable of range expansion, it is most likely to come from habitats modified by man. On the other hand, the decreasing northern species are mainly species of the taiga. It seems obvious to me that the taiga species have mainly decreased due to splitting of forests and cutting of old forest areas, not due to climatic shifts. As forestry has had a destructive character in northern Finland (see Järvinen et al., 1977), it is not surprising to find that, in contrast to southern Finland, many northern forest birds show major population decreases in recent decades (Järvinen & Väisänen, 1978 c; see also Järvinen et al., 1977, and Järvinen & Väisänen, 1977 b).

Indeed, it seems that a major cause of the remarkably dynamic patterns observed in the Finnish bird fauna is an increase of species well-adapted to environments modified by man, and a decrease of species requiring wide expanses of natural habitats.

Peatlands are another major habitat for land birds in Finland. Heikinjärvenneva, a peatland area in Central Finland, provides us with interesting data. Heikinjärvenneva is an *aapa* fen (e.g. Moore & Bellamy, 1974) growing few trees. As the peat layer grows slowly, usually less than 1 mm per year, succession is negligible. This area of about 2.5 km^2 has been studied by several ornithologists since 1954. The breeding bird fauna has changed very much (Järvinen, 1978). Nine species have certainly, and eight species have probably increased since 1954. One or two species have decreased, and it seems certain that these decreases were not caused by increased competition pressure. About ten species have been apparently stable. Many of the increasing species have also

increased elsewhere in Finland in recent decades, and these species have thus reached Heikinjärvenneva in the course of their general range or habitat expansion. As the breeding habitat has not changed, improved conditions in the winter quarters (e.g. possible decrease of hunting) and, as regards certain species, population pressure from other Finnish habitats (e.g. eutrophic lakes) are the probable causes of the great changes. Climate seems to be ruled out by climatological data and the fact that both northern and southern species have increased.

The example of Heikinjärvenneva shows that similar habitats do not always support similar communities; the community was obviously far less densely packed with species in the 1950s than in the 1970s. Heikinjärvenneva is not unique in this respect (see Kumari, 1972, for similar results in Estonia). This is direct evidence against the idea that most bird communities are saturated. Similar evidence has emerged from field experiments: if nest-boxes are introduced, fantastic numbers of hole-nesting birds invade most North European forest communities without any effects on other coexisting species (e.g. Enemar & Sjöstrand, 1972; cf., however, Hogstad, 1975). The lesson of these experiments is, however, not perfectly clear, as the resource spectrum was changed through the introduction of nest-boxes, and competition may require long time periods before it produces measurable effects.

My next example comes from a northern island group, the Åland Islands in the Baltic. They were surveyed ornithologically in the 1920s and 1930s, and again in the 1970s. Two extinctions (0.04 species/year), but 8—18 immigrations (0.16—0.36 species/year or about 1 % of the mainland species pool per year) were observed during 50 years (Haila et al., 1979). When the extinctions and immigrations were compared with long-term trends of the same species on the Finnish mainland, we observed that both of the extinct species had decreased on the mainland, while all but one of the immigrants had increased. Thus changes in mainland population pressure are an important determinant of species turnover on northern islands, for many temperate (mainly migrant) species are ready to disperse.

The Åland Islands show us another important principle of faunal dynamics. It seems obvious that increasing species are able to produce many colonists due to increased population pressure, and the high number of immigrants may be an explanation for the success of the colonizations observed (see also Diamond et al., 1976). On the other hand, decreasing species probably do not produce many colonists, and it is striking that none of the successful colonists of the Åland Islands was a decreasing species. This principle also emerges from studies of community dynamics of the Krunnit Islands (Väisänen & Järvinen, 1977) and Heikinjärvenneva (Järvinen, 1978).

Constraints of community change

Speculations and studies of the causes of population trends in single species are both fascinating and important, but similar problems may also be posed at the community level. Are there community-level constraints to community dynamics? The same problem may also be formulated by asking whether the communities are, in any sense, at equilibrium (see Järvinen, 1978).

I think an important principle in studying long-term dynamics of northern communities emerges from the above review: we have to look at large geographical regions, not

just certain well-defined areas (e.g. habitat islands, such as Heikinjärvenneva, or true islands, such as the Åland Islands).

Another important principle is evident from the quantitative measurements: important changes need not be rapid. For example, if a population increases only 2 % per average year, it is going to double in 35 years. It is thus impossible to conclude that a community is at equilibrium, unless it is studied for decades.

It seems that the best chances for finding general constraints of community change exist in studies of large areas. A line transect of about 50 km censused in 1936 (Kalela, 1938) was censused again in 1977, and the results suggested, as other line transect studies, major changes in the avifauna of southern Finland (Järvinen & Väisänen, 1978 b, 1978 c): total density had increased from about 110 to 190 pairs/km^2, or more than 70 %. However, the biomass of the breeding bird fauna (only adult birds included) increased by about 10 % only, from 20 to 22 kg/km^2 (Järvinen & Väisänen, 1978 c). This constancy of avian biomass in large areas seems to be of general validity in the whole of Finland in the past 30 years (Järvinen & Väisänen, unpublished). This is remarkable, as dramatic population changes have been characteristic of the period. The results may be interpreted as follows. Average productivity of large areas has probably not greatly changed in recent decades, because productivity tends to be correlated with climate (e.g. Rosenzweig, 1968). It thus seems that birds consume a roughly constant amount of energy (here indicated by biomass) in ecosystems producing roughly constant amounts of energy, but major changes have occurred in the apportionment of energy among different bird guilds, among birds of different habitats, and among birds of different major strategies (e.g. migrants vs. residents; Järvinen & Väisänen, 1978 c).

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Species Turnover in Island Bird Communities

Jared M. Diamond

This article considers species turnover on islands, along two very different time scales: (1) short-term turnover revealed by annual breeding censuses; (2) long-term turnover in evolutionary time, as revealed by degree of faunal endemism.

Short-term turnover

Sequences of annual breeding censuses on islands reveal frequent local extinctions (when a species breeds in some year but not in the next year) and immigrations (when a species breeds in some year but not in the previous year). Such censuses have been carried out by us on the California Channel Islands, and by numerous observers on European islands, such as the Farnes and Skokholm off Britain or Helgoland off Germany. On many islands the breeding species, and often the number of pairs of each species, are known for 10—40 consecutive years. Examples of the conclusions about turnover that these censuses permit include the following (for details, see Diamond, 1969 and 1971; Terborgh & Faaborg, 1973; Jones & Diamond, 1976; Diamond & May, 1977; Diamond & Jones, 1978):

Island populations fluctuate in numbers from year to year, just as do mainland populations (Fig. 1). Sometimes an island population disappears completely ("E" in Fig. 1) and may eventually be reestablished by immigrants ("I" in Fig. 1). The uppermost two species depicted in Fig. 1 went extinct and reimmigrated repeatedly in the course of 16 years. Had that island (Calf of Man) been surveyed only in 1959 and 1974, one would have concluded no turnover in the Stonechat *Saxicola torquata,* since it bred both in 1959 and 1974, whereas there were actually two extinctions reversed by two immigrations in the intervening years; and one would have concluded only one case of turnover in the Wheatear *Oenanthe oenanthe,* since it bred in 1974 but not 1959, whereas there were actually three immigrations reversed by two extinctions in the intervening years. Thus, censuses at intervals greater than one year tend to underestimate turnover.

Fig. 2 illustrates, for the British island of Lundy, how steeply the apparent turnover rate T decreases with the number of years t between censuses. The true turnover rate at a 1-year interval is 9.4%/year, but the apparent rate calculated from censuses several decades apart is only 0.7%/year! For all islands that we have studied, surveys spaced more than a decade apart underestimate turnover by about an order of magnitude, because of undetected immigrations and extinctions of the same population offsetting each other in the intervening years.

Turnover rates for the several dozen European and North American islands studied all fall in the range 1—20%/year. These relative turnover rates decrease with increasing island area, because larger islands support larger populations which are less likely to go extinct.

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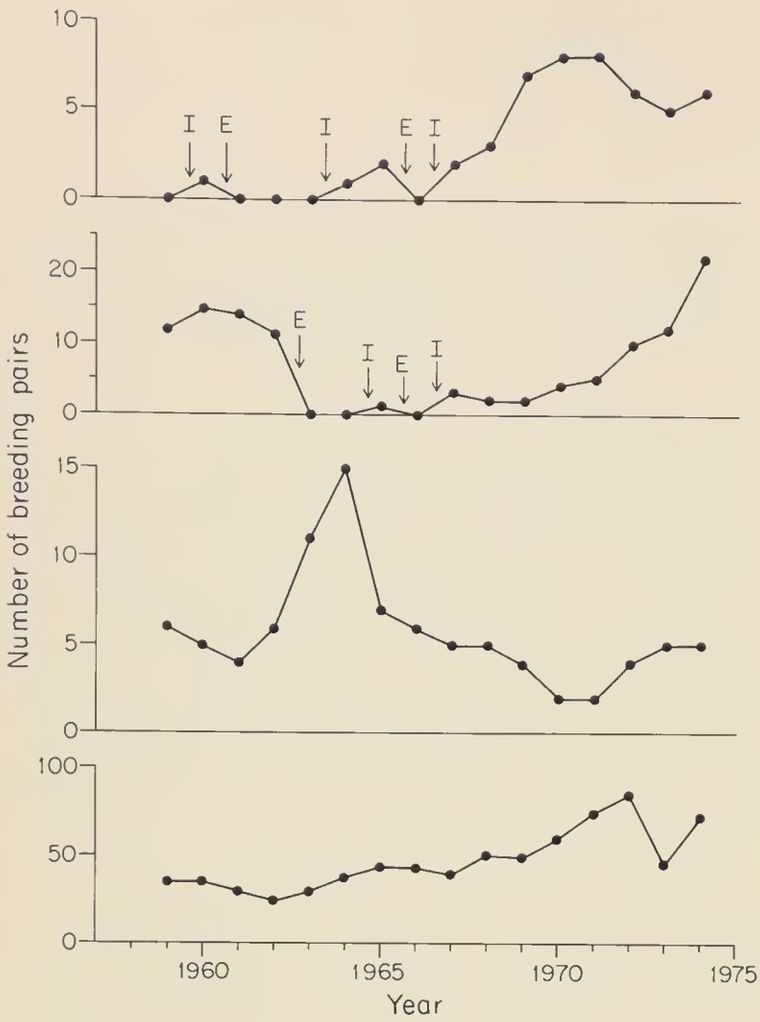

FIGURE 1. Number of breeding pairs of four bird species on Calf of Man, a small British island, as revealed by annual breeding censuses from 1959 to 1974. From top to bottom the species are: Wheatear *Oenanthe oenanthe*, Stonechat *Saxicola torquata*, Skylark *Alauda arvensis*, and Meadow Pipit *Anthus pratensis*. E and I indicate, respectively, an extinction of a local population (i.e., an instance in which there was a breeding population one year but not in the succeeding year) and an immigration (i.e., an instance in which there was a breeding population in one year but not in the previous year).

Despite this considerable species turnover, species number on islands remains relatively constant in the absence of major environmental disturbance, bacause immigrations on the average balance extinctions. For example (Fig. 3), on the British island of Skokholm species number from 1928 to 1974 fluctuated within relatively narrow limits (generally 9—15 species), despite an average turnover rate of 9.5%/year.

These figures do not mean that every species on an island has a 1—20% chance of turning over in a given year. If so, no island population would survive long enough to differentiate to the level of an endemic taxon. Instead, different species turn over at very different rates on the same island. Some species breed every year, while some mainland species never breed on an island—in either case there is no turnover. Other species breed on an island in some but not all years and do turn over—in some cases, as often as once every other year on the average. Large islands have more populations that breed every year, without turning over, than do small islands. The reason is again that large populations are less likely to go extinct. One therefore expects that large islands should have relatively more populations that survive long enough to differentiate to the level of an endemic taxon. We shall see that this prediction is confirmed (Fig. 4).

Why are some populations more prone to extinction than others? The most obvious correlate is that extinction probability decreases steeply with population size. Hence species with large territories and species with specialized habitat requirements are especially prone to extinction. In addition, species differ in their proneness to extinction at

a given population size. For example, on British islands populations of Raven *Corvus corax* consisting of only two or three pairs may survive uninterruptedly for decades, while populations of Lapwing *Vanellus vanellus* or of Skylark *Alauda arvensis* with the same average number of pairs go extinct and recolonize repeatedly. Species in which each individual is long-lived tend to have more long-lived populations than species in which individual are short-lived, but other demographic parameters are also important. FRITZ's paper in this symposium illustrates these principles, by showing how the lifetime of a Spruce Grouse population can be predicted from the number of breeding pairs, through knowledge of two demographic parameters, the birth and death rate.

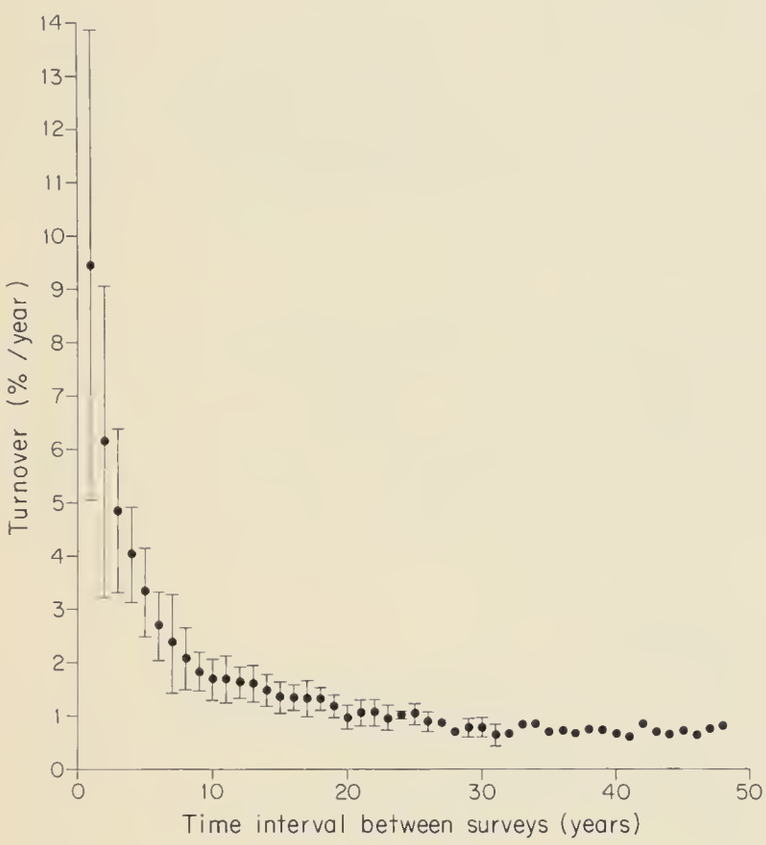

FIGURE 2. Apparent turnover rate of the breeding land bird community on the British island of Lundy, as a function of time interval between surveys. Lundy has been surveyed nearly annually from 1922 to 1974. For each pairwise combination of census years, turnover (in units of %/year) was calculated as $100 (I + E)/(S_1 + S_2) t$, where I is the number of apparent immigrations and E is the number of apparent extinctions revealed by comparison of species lists for the two years; S_1 and S_2 the number of breeding species in the earlier and later census year, respectively; and t the number of years between censuses. The calculation was carried out for all pairs of census years corresponding to a given time interval, and the resulting average values and standard deviation of the turnover rates plotted as the solid point and vertical bars, respectively.

At this point two common misconceptions about turnover deserve mention. First, some authors seek to dismiss most cases of turnover as being due somehow to effects of man. Certainly, man can cause turnover either directly (by shooting birds and destroying nests) or indirectly (by modifying habitats), as illustrated by examples from the California Channel Islands and European islands in recent years. However, detailed observations of populations on these islands fail to suggest a link between most cases of turnover on these islands and man. Instead, most turnover seems to reflect either random changes in small populations, or else environmental effects such as cold winters, warm migration periods, and wet summers. Indeed, on the California Channel Islands man's overall effect during this century has apparently been to reduce turnover below the values that would have been observed in the absence of human disturbance, by differentially eliminating rapidly turning-over populations (JONES & DIAMOND, 1976).

The other misconception is that most turnover is "just" an appearance and disappearance of transient breeding populations that do not represent genetic isolates and that are tacitly considered uninteresting. Of course, most turnover observed in a study lasting a few years necessarily involves short-lived populations. Some species do

FIGURE 3. Number of breeding land bird species on the British island of Skokholm, based on censuses in each year from 1928 to 1967 except for the war years of 1940—1945 (shown as question mark).

have many short-lived populations but few genetic isolates, and this fact is not uninteresting but rather essential to understanding the genetic structure of such species. The longer the time-scale of the study, the more likely becomes observation of turnover of long-lasting populations. We shall now see that the turnover of very long-lived populations on an evolutionary time scale fits some of the patterns that we have just considered for short-term turnover.

Long-term turnover

Turnover on an evolutionary time scale cannot be observed directly, but it can still be inferred from frequencies of endemic forms (MAYR, 1965). It is a familiar fact that many islands have endemic bird taxa, such as endemic subspecies, species, or genera. High endemism means low extinction rates, because a population must survive a long time—perhaps hundreds or thousands of years—to differentiate to the level of an endemic subspecies, and it must survive even longer—perhaps thousands or millions of years—to differentiate to the level of an endemic species or genus. Some islands have many endemic forms, some only a few. Occasionally this is for trivial reasons.: there are unlikely to be many distinctive bird endemics on islands that recently rose from the sea (e.g., Surtsey), or that were recently covered with glaciers (e.g., Iceland), or that were recently connected to a nearby continent (e.g., Trinidad, Ceylon). But there are still large differences in bird endemism among unglaciated Pacific islands millions of years old. For example, Hawaii, the Galapagos, New Guinea, and New Zealand are famous for their distinct endemic birds, while Fiji, the Solomons, Bismarcks, and New Hebrides have few.

Degree of endemism also differs among populations on the same island. For example, New Caledonia is a geologically old island on which volcanism ceased about 80

million years ago, and it has many old distinct plants and insects. New Caledonia has 71 breeding land bird species, which are of various ages as reflected in their various degrees of endemism (MAYR, 1941). One New Caledonian species, the Kagu *Rhinochetus jubatus,* belongs to an endemic family; four belong to endemic genera; 14 are endemic at the species level; 26 are endemic only at the subspecies level; and 26 are not even subspecifically distinct from ancestral populations on Australia and New Guinea. Thus, although New Caledonia is an old island, 52 of its 71 present bird species arrived so recently that they are not even specifically distinct. The New Caledonian avifauna is a mixture of a few old populations like the Kagu, that have persisted for millions of years, together with many young populations that turn over so rapidly that they have little chance to differentiate. (In principle, high gene flow from New Guinea or Australia could also explain failure to subspeciate. However, this consideration cannot apply to differentiation past the subspecies level, since so few vagrant individuals of extralimital subspecies have been recorded in New Caledonia, and since so few of New Caledonia's 19 endemic species that are reproductively isolated from outside populations have survived long enough to become members of endemic genera and families. An additional problem is that endemic taxa need not give a measure of extinction rates if they were relicts of former widespread taxa rather than if they differentiated in situ, but we favor the latter interpretation of most endemic Pacific land bird populations).

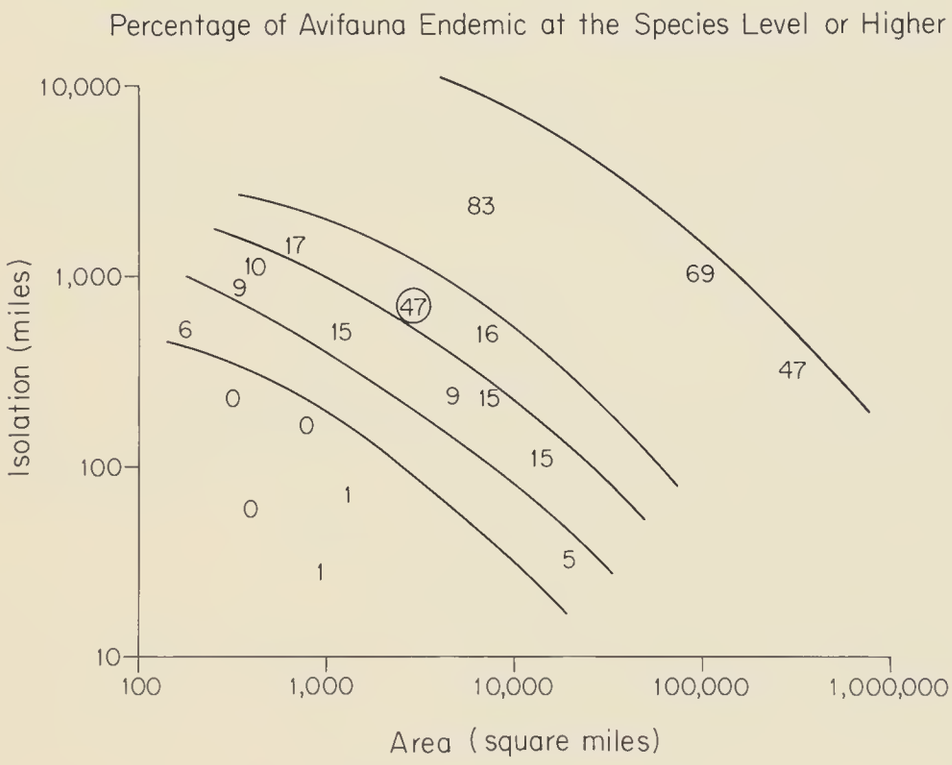

FIGURE 4. Numbers on the graph give, for some Pacific island or archipelago, the percentage of its breeding land bird species that are endemic at the level of full species or higher. Location of number gives the island's area (square miles, abscissa) and distance from nearest major colonization source (miles, ordinate). For example, 16 % of the species of Fiji, with an area of 7055 mi^2 and distance of 520 miles from the New Hebrides, are endemic full species or belong to endemic genera. Curves are drawn by hand to group islands with similar endemism. Circled "47" refers to the Galapagos Islands, which have higher avifaunal endemism than do southwest Pacific islands (because neotropical birds, the source for the Galapagos, are poorer colonizers than New Guinea birds, the source for the southwest Pacific).

We expect that the percentage of old, endemic populations in an island avifauna will be a function of the island's area and isolation: large or remote islands will have lower extinction rates and hence a higher percentage of old populations. To test this prediction, Fig. 4 plots, for the main archipelagoes and islands of the Pacific, the percentage of the island's bird species that are endemic at the species level or higher, as a function of the island's area and its distance from the nearest major colonization source. The figure yields two main conclusions. First, the percentage of endemic species increases with increasing area (i.e., from left to right in the figure), because extinction rates decrease with increasing area. Second, the percentage of endemic species increases with increasing isolation (i.e., from bottom to top in the figure), because immigration rates decrease with distance. (Although percentage of endemics is directly related only to extinction rates and not to immigration rates, high immigration increases extinction rates by increasing equilibrium species number). The only Pacific islands with a high percentage of endemic bird species are the huge, somewhat isolated islands of New Guinea (47%), New Zealand (69%), and Australia (49%), and the medium-sized, very remote Hawaiian (83%) and Galapagos (47%) archipelagoes. Very remote but small archipelagoes, such as the Marquesas (9%) and Societies (17%), and large but close archipelagoes and islands, such as the Solomons (15%), Bismarcks (5%), and New Caledonia (15%), have only a modest percentage of old endemics. Small and close islands, such as the Kei islands (0%) and Karkar (0%), have no old populations at all, because all bird populations on such islands turn over rapidly and no bird populations survive on them for millions of years.

Acknowledgments

It is a pleasure to acknowledge our debt to T. Reed and many other colleagues, for information about European bird distributions.

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Species Reduction in Remanescent Woodlots in Southern Brazil

Edwin O. Willis

Preston's warning (1962) that isolated small patches of habitat lose species by internal rearrangement, even when man does not interfere from outside, was confirmed by censuses of birds of Barro Colorado Island, a forested hilltop isolated by Gatun Lake during construction of the Panama Canal about 1914 (Willis, 1974). Many of the species that disappeared were birds of second growth, but others were forest hawks and birds of the forest floor. To see how other isolated forests lose species, I censused the avifaunas of three isolated woodlots on the subtropical São Paulo plateau in southeastern Brazil from 1975 to 1978.

Study areas and methods

Near the Tropic of Carpicorn, the subtropical São Paulo plateau slopes west from the Serra do Mar to the Paraná River valley. Sugar cane, and after 1840, coffee culture (Hueck, 1966: 1978), resulted in widespread deforestation. One of the largest patches of forest remaining is 1400 ha at 500—600 m elevation in the pastures of Fazenda Barreiro Rico, at 22° 45′ S and 48° 09′ W. The forest is on sandy soil, and has been subject to some tree removal and windthrow, but is otherwise a fairly typical hilltop woodland. Two smaller tracts of forest at 620 m elevation on Fazenda Santa Genebra, 250 ha at 22° 49′ S and 47° 07′ W and 21 ha at 22° 50′ S and 47° 04′ W, were also censused. Both include small creeks and swamps. Because of tree removal and some second growth areas, they are similar in appearance to the Barreiro Rico woodland despite better-watered conditions and better "terra roxa" latosols.

Two methods were used: general censuses, walking to all parts of the woodlots; and one-hour censuses, intensive recording of all birds seen or heard on standard routes. One-hour censuses resulted in high detection rates of individuals but otherwise gave much the same results as general censuses. General censuses totaled 550.4 hours at Barreiro Rico (B), 444.3 hours at the large Santa Genebra tract (S), and 205.0 hours at the small one (Unicamp, or U).

Census results

I found 202 species at B, 146 species at S, and 93 at U. At 200 hours of observation, some 180 species were recorded for B, 130 for S, and 90 for U. Originally some 60 other species should have been in all forests of the region, but 20—40 edge species would have been absent; totals would have been near 220 species in each of these areas. Collections in 1957—64 at B, available in the São Paulo Museum, include 10 vanished forest species, mostly large frugivores: *Tinamus solitarius, Triclaria malachitacea, Baillonius bailloni, Selenidera maculirostris, Procnias nudicollis, Cacicus haemorrhous.* The bellbird was still present in 1970 (D. Ewert, pers. comm.).

Complete lists and analyses of species will be published elsewhere. Numbers of individuals per 100 hours of general censuses are indicated for different foraging groups or

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guilds in Table 1. Very few species that bred in a small woodlot were absent from a larger one, so that small woodlots helped conservation mainly by repeating species in a different location.

TABLE 1: Birds of three São Paulo Woodlots

	Species			Individuals/100 h		
Large Forest Frugivores	17	4	3	383	154	21
Small Canopy Omnivores	10	8	5	223	241	86
Small Understory Omnivores	9	7	6	344	283	79
Edge Frugivores/Omnivores	22	18	16	120	385	306
Ground Frugivores	7	5	2	230	281	172
Large Nocturnal Carnivores		1	2		1	1
Diurnal Carnivores	9	5	3	39	42	21
Carrion Eaters	3	1	1	17	—	—
Trunk and Twig Insectivores	15	9	4	177	139	96
Large Ground Insectivores	10	5	1	198	6	12
Small Ground Insectivores	7	5	4	165	283	279
Small Understory Insectivores	12	11	8	591	751	457
Forest Tangle Insectivores	8	4	1	125	108	84
Midlevel Insectivores	11	9	5	285	496	69
Small Treetop Insectivores	8	9	6	221	322	80
Edge Insectivores	18	15	14	156	305	103
Aerial Insectivores	7	7	5	88	90	47
Nocturnal Insectivores	8	5	2	37	14	10
Nectar and Insect Eaters	12	11	4	66	58	20
Edge Seedeaters	9	7	2	83	48	7
Totals	202	146	93	3 548	4 007	1 950

Birds of two groups were especially likely to disappear in small woodlots: large frugivores of the canopy and large insectivores near the ground. A few edge frugivores and a few ground frugivores partly compensated for loss of large frugivores by increasing in small woodlots. A few large owls *(Tyto alba* and *Pulsatrix* sp.), perhaps feeding on nocturnal mammalian ground frugivores, were noted only in small woodlots. Squirrels and large lizards *(Tupinambis* sp.) were commoner on or near the ground in small woodlots. Monkeys, arboreal frugivores, also decreased in diversity in small woodlots. No guild increased in diversity in a small woodlot except for the owls, even when more individuals were present in a small woodlot.

Density compensation was not noted in the smallest woodlot: 35.5 birds per hour in B, 40.1 in S, and 19.5 per hour in U. (In one-hour censuses, there were 79.9, 87.5, and 50.0 birds per hour, respectively.)

Summering migrants were more abundant in the intermediate-sized woodlot at 10 % of the birds per hour in general censuses in S, 6.9 % of those in B, and 5.6 % of those in U. In B, there were 13 species, in S 12 species, and in U 9 species. Wintering migrants were 5 species in B, 5 in S, and 2 in U; only the flycatcher *Contopus cinereus* of midlevels was common. Many migrants are from the families Cotingidae and Tyrannidae. None came from the forest interior, probably because these forests lose only some canopy foliage in winter. In the dry winter of 1975, the forest-interior *Empidonax*

euleri was uncommon and may have migrated. In the dry summer of 1978, nearly all summering species disappeared by January, and many failed to breed.

Vagrant species, including transient migrants, numbered 22 species in the two large woodlots and 15 in the smallest one. Some vagrants were winter-wandering facultative frugivores *(Elaenia* spp. of the Tyrannidae and *Turdus* spp. of the Turdidae, for example); they probably exploit and thus encourage the July to September fruiting peak in southeastern Brazil (Davis, 1945).

Many species found in the woodlots (140 of 216 species) are known to cross open areas, and more may do so. Occasional singing unmated birds, apparently wanderers from the nearby forests of the Serra do Mar, reached the small Campinas woodlots but not the more distant Barreiro Rico: *Cranioleuca pallida, Batara cinerea,* etc. Only among ground and tangle insectivores were most species unlikely to cross open areas. Large fruiteaters, small understory insectivores, and trunk-foraging birds averaged about half species known to cross open areas. Nonwandering species were less diverse in small woodlots: 74 species (37 % of the avifauna) at B, 38 at S (26 %) and 19 at U (20 %).

Passeriform and tyrannoid tyranniform birds increased in diversity in small woodlots: 21, 26 and 28 % for the former in B, S, and U; 27, 27 and 32 % for the latter. Furnarioid tyranniforms (15, 14 and 10 %) and other nonpasseriform birds (37, 33, and 39 %) decreased in small woodlots. The first two groups favour edges or temperate-zone woodlands and include many migratory species; the last two groups often do best in continuous vegetation or are large (hawks) or food specialists (parrots).

Frugivorous species decreased from 9 to 6 % of species in the two small woodlots, while omnivores were 23 % in the two large woodlots but 27 % in the smallest one. Insectivores were 51 % in the largest woodlot, 54 % in the others. Carrion eaters and carnivores (5—6 %), nectarivores (5—8 %), and granivores (2—5 %) did not show consistent changes in proportions from small to large woodlots.

Discussion

Reduction of species in small woodlots resulted in disproportionate losses of large fruit-eating birds and of large insectivores of the understory, so that edge omnivores and small insectivores became proportionately (or, in numbers of individuals, absolutely) more important. This led to an increase in passerine and tyrannoid tyranniform proportions in small woodlots. The avifaunas of small woodlots thus became more like avifaunas of temperate zones, except that migrants were uncommon as nonmigrants in the smallest woodlot.

Losses of large understory insectivores probably result from large home ranges or low population densities, so that local extirpation becomes very probable in small woodlots in years of unfavourable food supply (often due to climate) or predation. Large woodlots often will have a dry (wet) area for refuge in wet (dry) years, while small ones often will not. Losses of large frugivores, which can wander readily between woodlots, may be due to a different problem: failure of small areas to provide a year-round set of fruiting trees, especially when local failures of fruiting can occur. Such birds could perhaps be raised in zoos or provided fruit by planting or artificial feeding if deforestation continues in such areas as the São Paulo plateau. This kind of solution

appeals to many Brazilians, but funds and knowledge are seldom sufficient; over time, buying land for reserves is less expensive. Large insectivores are best preserved by leaving large wooded reserves and corridor zones between the reserves. This strategy would also preserve most of the large frugivores without artificial human effort; but it requires an active land-control policy.

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Post-pleistocene Changes in the Distributions of African Montane Forest Birds

R. J. Dowsett

Introduction

Moreau (1966) discussed possible changes in the African avifauna during and subsequent to the Pleistocene. Recent palaeoclimatological research (Livingstone, 1975) suggests that the timing and sequences of vegetational changes during the past 10,000 years may differ in several respects from Moreau's assessment. Further radio carbon dated pollen analyses should clarify this. Meanwhile, it is useful to consider ways in which the distributions of some African montane forest birds may have changed, without commitment to chronology. This is essentially a review of topics which will be discussed in greater detail elsewhere.

Desiccation and fragmentation

It is probable that the African montane forests were most extensive during a past period of high rainfall. Subsequent desiccation of the environment has restricted the distribution of evergreen forest biomes, and those that remain today are often greatly fragmented and reduced in area, expecially as a result of increased human land abuse. There is at present no evidence for any significant forest expansion during the past 10,000 years.

The fragmentation of high altitude forest has produced a corresponding fragmentation of the distribution of montane forest birds, which species are mostly stenotopic and unadaptable. Moreau (1966: 191, 193) gives as examples of widespread species the Starred Robin *Pogonocichla stellata* and Mountain Babbler *Alcippe abyssinica*, which are nevertheless surprisingly absent from some montane areas. I have discussed elsewhere the relationships between these isolated montane populations (Dowsett, 1971; in press), and have stressed their essentially sedentary and stable nature. In contrast, the most dynamic of oceanic island colonists are species of secondary growth (MacArthur et al., 1972). Clearly the prognosis for the continued existence of many forest avifaunas is poor, without the establishment of effective reserves in which control of fire and felling is of paramount importance. Such reserves should follow the guide-lines of Diamond (1976), with additional regard for the preservation of a wide and continuous altitudinal range of habitats.

The altitudinal distribution of forest birds

Moreau (1966: 47) considered that a wetter climate would have lowered the limit of montane biomes from the present level of about 1500 m to some 500 m above sea-level. He postulated that species that are now confined to high altitudes would have occurred much more widely, whereas typical lowland species would be more limited in distribution than now, being "incapable of living in a montane climate". Livingstone (1975)

Livingstone Museum, P.O. Box 498, Livingstone, Zambia.

also suggests that some montane birds could have ranged to lower altitudes "into the lush evergreen forests of 10,000—7000 BP". It is not proven that significant physiological differences exist between montane and lowland bird species, and several species typical of lower altitude forests also occur on some mountains. Table 1 shows the proportions of lowland species in some montane avifaunas, the data being taken from Keith et al. (1969), Prigogine (1974), Dowsett (pers. obs.) and Diamond (1972) respectively. Three of these samples are from areas in which lowland and montane forests are continuous, the exception being the Nyika in Zambia.

Table 1: Lowland elements of some montane forest avifaunas

Locality	Montane endemics	Lowland element	Total no. montane species (100 %)
Impenetrable forest, Uganda	83 %	17 %	69
Itombwe, Zaire	65	35	99
Nyika Plateau, Zambia	57	43	46
Karimui, New Guinea	43	57	35

Judging by the situation elsewhere in the tropics — for example in New Guinea (Diamond, 1972) — there could have been in Africa a wide variety of altitudinal ranges occupied by different species. If so, then the present day division of species into montane, intermediate and lowland (e.g. Prigogine, 1974) may be largely artificial. Diamond (1972: Figure 5) showed that, in an undisturbed forest area of wide altitudinal range, the decrease of species diversity with increasing altitude is apparently progresive. Unfortunately few continuous areas of lowland and montane forest remain in Africa. Most high altitude forests are now isolated from their lowland counterparts, or at the most joined tenuously by narrow strips of riparian forest.

Preliminary analyses of the African montane avifaunas suggest that there exist peaks in the numbers of montane species present at just below 2000 m. It is not clear if this is the reult of biased sampling, or if it reflects a greater ecological complexity in the African mid-altitude forests in comparison to those of New Guinea.

Species diversity in Central African forests

The montane forests of the Nyika Plateau in Zambia and Malawi (at an altitude of over 2100 m) contain few lowland species of bird. All seven Turdidae are confined to high altitudes in this part of Africa, and only one of the four Columbidae (the Tambourine Dove *Turtur tympanistria*) occurs widely in lowland forest. Within both families there is a segregation of species by habitat or size. The two ground feeding doves, for example (*T. tympanistria* and the Cinnamon Dove *Aplopelia larvata*), differ in body mass by a factor of 2. In New Guinea Diamond (1973) found a factor of 1.5 of body mass separated most of the frugivorous doves that might be expected to compete.

In these and other families in the montane forests, most genera are represented by only a single species (an exception being the artificially large sunbird genus *Nectarinia*). Furthermore, a large proportion of the Turdidae genera are unrepresented in lowland forests. There are very few examples of the kind of intra-generic altitudinal species

replacement found by Diamond (1973) in New Guinea, although Prigogine (1974: 86) gives examples from the extensive forests of eastern Zaire. The conclusion to be reached is that there has been widespread extinction of forest species in the degraded areas that now exist between the relic montane and lowland forest of central Africa.

Table 2: Bird species diversity in some central african forests

	Total no. caught	Species: caught[a]	% of total	D_s: Species diversity[b]	Dominant species
Nyika, Zambia: 1975	100	14	31 %	5.650	*Pogonocichla stellata* 36 %
1977	108	18	40	6.983	*P. stellata* 31 %
Isombu, Zambia	108	23	66 %	6.640	*Andropadus virens* 34 %
Mwombezhi, Zambia	100	24	86	11.939	*Cossypha bocagei* 15 %
Mafinga Mts., Zambia	101	25	54 %	13.263	*Batis capensis, A. virens* 14 %
Mangochi Mt., Malawi	122	21	68	13.550	*P. stellata, Nectarinia oliv.* 11 %
Misuku Mts., Malawi	126	23	56	14.285	*B. capensis* 15 %
Ufipa Plateau, Tanzania	100	34	94	22.026	all < 10 %
Rungwe Mt., Tanzania	141	34	79	22.321	all < 10 %

[a] Number of species in a sample of the first 100 individuals caught in mist nets.
[b] Bird species diversity, based on 100-bird samples, using the formula $D_s = -\sum_i p_i^2$.

It is difficult to quantify the species diversity observed in most African forests, as many factors make normal census techniques difficult to implement. However, I have determined the species diversity observed in most central African forests (two lowland and six montane), on the basis of samples of the first 100 birds caught in each of them in mist nets (Table 2). Most samples show the dominance of one or two species (in montane areas usually *Pogonocichla stellata*), with D_s values (Formula: $D_s = -\sum_i p_i^2$) ranging from 5.6 to 14.2. Some values of up to 22.3 suggest a much greater species diversity, and these are found in areas where montane forest is in close proximity to lowland and riparian forest or deciduous woodland (e.g. Mt. Rungwe in Tanzania). These data also suggest that isolated high altitude forests have received no increase in species totals as a result of the vegetational changes that have eliminated mid-altitude forests. Rather, the mid-altitude avifaunas have disappeared completely from such areas through a lack of adaptability. The remaining montane avifaunas appear to be stable communities, long-established and with a minimum of interspecific competition.

Some barriers to forest bird dispersal

Even if future evidence shows that some forest birds are not as sedentary as supposed, there are now some very considerable barriers to their dispersal. Indeed, it is likely that some barriers have been effective for a very long time, and that the patchy distribution we see now in many species has been long established. For example, Benson et al. (1970: 51) mention a few forest species known only from the eastern side of the Nyika Plateau, and apparently absent from the western side. It might be thought that their absence is because of the extensive tracts of grassland now separating forests in that area. But although such grasslands have long existed on the Nyika, their exten-

sion has been relatively recent (whatever the actual time scale involved). It seems likely that such birds have always been absent from the west, and that some other barrier to distribution may have existed in the past, possibly climatic or topographic.

The rift valleys of Africa might be thought obvious barriers to the spread of any forest species that is sufficiently mobile, because their altitude and climate preclude the growth of any extensive evergreen vegetation. Such valleys are now barriers not only to forest species, but to any birds that are normally absent from such dry deciduous woodlands as *Acacia* and mopane. It has been suggested by Benson et al. (1962: 172—178) that the Luangwa rift in eastern Zambia has been especially a barrier to many forest species which are now absent from one side or the other. I have examined the examples they give, in conjunction with data from the species distribution maps of the *Atlas of the Birds of Zambia* (Dowsett, in prep.). I find that for most such species there are barriers to distribution other than the Luangwa rift, as the following selection demonstrates.

Ross's Violet Loerie *Musophaga rossae* is usually associated with evergreen forest, although it also occurs in adjacent deciduous woodland. Although there are no confirmed records east of the rift, there is a recent report from northern Malawi. The Black-backed Barbet *Lybius minor* has a similar distribution, except that it clearly does occur east of the upper Luangwa, where the rift is least developed as a barrier. But its absence from further south than the Nyika area in eastern Zambia is clearly influenced by a barrier other than the rift, probably that part of the plateau which is dissected by mopane woodland and where suitable riparian forest is lacking.

The Purple-throated Cuckoo Shrike *Campephaga quiscalina* is a species whose eastern distribution falls far short of the rift. There are many apparently suitable forests in north-eastern Zambia west of the rift from which it is absent, and although the reasons for this are unknown, it does explain its absence from eastern Zambia.

The Starred Robin *Pogonocichla stellata* is one of many species which occur in montane forest east of the rift but are apparently absent to the west. However, some other species do occur on both sides, for example the White-tailed Crested Flycatcher *Trochocercus albonotatus,* and so absences are likely to be the result of factors other than the existence of the rift, and are also likely to be long-standing.

I agree that elsewhere in Africa rift valleys may have had a more direct effect on forest bird distribution, as I have suggested in the case of the Shire valley (Dowsett, 1971). But clearly relatively insignificant features may have been important barriers in the past (Dowsett, 1974), and it is their past effect which is important, and not merely the situation as it appears today.

The deciduous miombo woodlands of central Africa are in a special category as barriers to forest species. Their avifauna ist discussed by Benson & Irwin (1966) and their vegetation by Fanshawe (1971). They now occupy what must once have been country covered by evergreen forest, during a past period of greater precipitation. Fanshawe (op. cit.) discusses in detail the effects of fire and cutting on several vegetation types, and in particular the re-establishment of evergreen forest when miombo receives effective fire protection for a period of 20 or 30 years. Such forest in northern Zambia is readily acceptable to evergreen forest birds. It seems highly likely that it is the great increase in human land-abuse in central Africa during the past few centuries, in partic-

ular the now annual occurence of uncontrolled fires, that has reduced to deciduous woodland the large areas of evergreen forest which once joined the remnants of Angola to those of north-eastern Zambia. Forest species have retreated to refuges, mainly in riparian growth where the water table is still high. As such refuges have diminished in size, so will have the number of bird species diminished, with many becoming extinct.

It is not clear if any of the present endemic miombo avifauna has a forest origin. Certainly some species have close relatives that are confined to evergreen forest (e.g. the weavers *Ploceus angolensis* and *insignis).* The Dusky Flycatcher *Muscicapa adusta* occurs today in both miombo and forest, and there are even resident montane populations. Other miombo species are in genera which are also well-represented in forest (e.g. the cuckoo shrikes *Coracina pectoralis* and *caesia*), although their relationships and evolutionary origins are still unclear. Few forest species can have adapted successfully to deciduous conditions, but there remains the possibility that some have done so.

Conclusions

The evidence available so far suggests that the forest bird populations of Africa are relics of a past era. Present human activities are eroding these refugia at a rate which precludes any natural expansion should the climate of Africa become appreciably colder and wetter in the future. Only ecological manipulation, and especially fire control, can preserve the montane forest blocks.

This accelerating habitat degradation is of more than aesthetic concern. The great stability of the forest avifaunas is of considerable evolutionary importance, as study of other continental and island biomes has necessarily been concerned with species living in a dynamic and ever-changing environment. This assessment of the possible changes in the montane forest avifaunas since the Pleistocene has been able to consider only circumstantial evidence, for the reason that we still know almost nothing of the population dynamics of tropical forest birds themselves.

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SYMPOSIUM ON FLOCKING BEHAVIOUR

9. VI. 1978

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Comments on the Function of Flocking in Birds

J. R. Krebs and C. J. Barnard

Introduction

Most of the emphasis in studies of flocking in birds during the past ten years has been on the function of flocks: the approach has been to try and assess quantitatively how individuals benefit from associating with members of their own or different species. In contrast, much of the earlier literature on flocking concentrated largely on

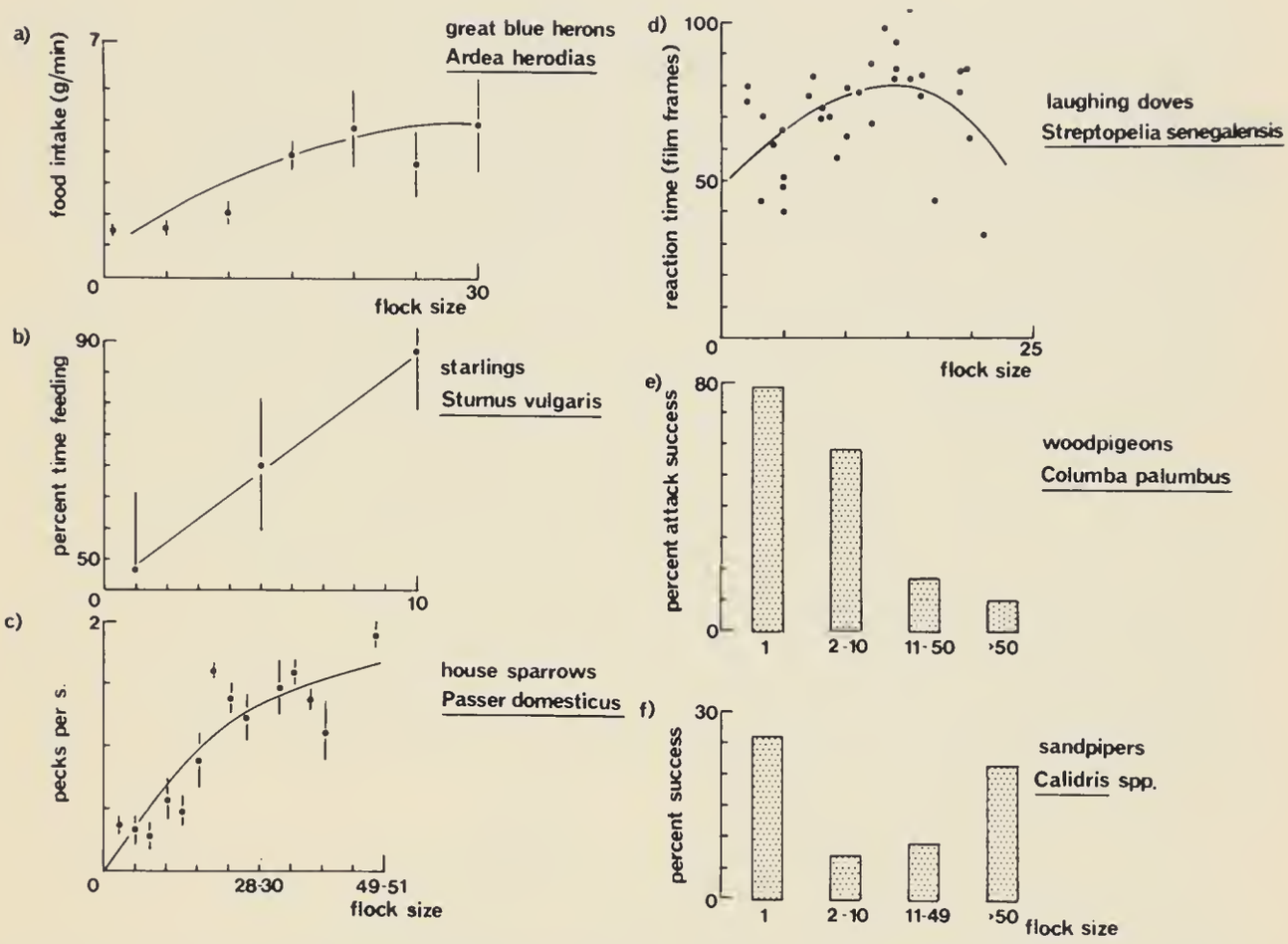

Figure 1. Six studies in which the benefit of flocking has been measured quantitatively. (a) Rate of food intake increases with flock size in Great Blue Herons (Krebs, 1974) up to a group size of about 20 birds. (b) Captive Starlings in larger groups spend a higher proportion of their time feeding and less time scanning for predators (Powell, 1974). (c) House Sparrows feeding in larger groups on farmland have a higher peck rate (Barnard, 1978). (d) There is an optimum flock size for detection of a approaching hawk model by Laughing Doves drinking at a water hole (Siegfried & Underhill, 1975). (e) The hunting success of trained Goshawk decreased with increasing size of the flocks of pigeons which they were attacking (Kenward, 1978). (f) There is an optimal flock size for sandpipers, at which a Merlin had the lowest percent success in attacking the group (Page & Whitacre, 1975). The lines in (a), (c) and (d) are fitted regressions (2nd order polynomial); the line in (b) is fitted by eye.

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mechanisms of flock cohesion and structure (Emlen, 1952; Crook, 1961), and attempts to link together flock structure, dynamics and function are only just beginning to emerge (Caraco, 1980).

Two main selection pressures favouring grouping in birds have been identified: individuals may benefit by increased feeding success or by avoidance of predators. These two benefits are not mutually exclusive as claimed or implied by some workers, and the decision of an individual to join or leave a flock should depend on an assessment of all the costs and benefits of being in a group. One of the important future areas of research on flocking will be to elucidate how individuals assess these trade-offs. Particular types of benefit could be brought about in a variety of ways (Bertram, 1978), for example the "feeding" advantage could result from mechanisms such as copying others to find good feeding places, or to find the best prey types. It could also result from disturbance of hidden prey, or even herding and other forms of cooperative hunting of prey which try to escape. These different mechanisms which result in a "feeding" advantage are likely to be associated with differences in flock structure and cohesion; to take an extreme case, species such as herons which may simply use flocks as an indicator of good feeding patches can be expected to have less cohesive and organised groups than predatory mammals which are cooperative hunters.

Figure 1a and 1b show some examples of both the feeding and anti-predator benefits of flocking; the results are all from studies which have compared some measure of success of individuals in groups of different sizes. The rationale is that if flocking has a measurable benefit, there should be an optimum flock size in which individuals do best. Three of the studies have shown an optimum flock size (Siegfried & Underhill, 1975; Page & Whitacre, 1975), or one in which benefit is at an asymptote (Krebs, 1974). The others have shown a positive correlation between flock size and benefit, and presumably the benefit must decrease again at much larger flock sizes than those studied.

In the remainder of this introduction to the flocking symposium we will discuss three criticisms which could be levelled at the type of study illustrated in Figure 1, and try to suggest some alternative approaches.

How to measure benefit

The first point, which we will exemplify by talking about the "feeding" benefit, is that there may be several ways to measure benefit. Studies of feeding success of birds in flocks of different sizes have usually assumed that benefit should be measured by an increase in peck rate or more precisely rate of food intake; alternative measures such as a reduction in the variance of rate of intake are generally ignored. Thompson et al. (1974) suggested on the basis of a simulation model that reducing variance of intake may be a more important benefit of flocking than maximising immediate success. An example of how this consideration can alter the interpretation of results is the work of Davies (1976) on Pied Wagtails *Motacilla alba*. Davies compared the peck rate of solitary birds feeding on a river bank and flocks feeding in a nearby flooded meadow. The flock birds did better in the very short term, achieving a higher rate of food intake than the maximum of solitary individuals. However conditions were only occasionally good enough for flocks to form on the meadow, and the solitary individuals which defended territories on the river bank had a more reliable food supply. A short term study might

have concluded that flock birds do better, but a longer term record would show that they do not.

Flocking has costs as well as benefits

The second point can also be illustrated by studies of the "feeding" benefit of flocks. SMITH (1977) found that the peck rate of grackles *Cassidix mexicanus* did not vary significantly with his index of flock size. This does not necessarily indicate that flocking has no benefit in terms of food intake; it might simply mean that there are disadvantages as well as benefits of flocking. The most likely disadvantage in feeding is interference between neighbours, as illustrated by GOSS-CUSTARD's (1976) finding that the peck rate of visually hunting Redshank *Tringa totanus* is negatively correlated with nearest neighbour distance. If we accept that interference is related to bird density in the flock and that there is also a feeding benefit dependent on flock size, we can see how feeding success may be independent of flock size (Fig. 2). The figure uses a modification of FRETWELL's (1972) model of habitat distribution, assuming that birds are free to join or leave flocks in order to maximise benefit. Suppose, for example, that the first birds to arrive in an area form a flock at the best feeding site. As more birds arrive, both flock size and flock density increase, and there may be a point at which it is just as advantageous for a new arrival to go to an unoccupied site and feed on its own or in a small group. If birds can accurately assess the advantage of joining different groups, the feeding success of individuals in all group sizes should be equal.

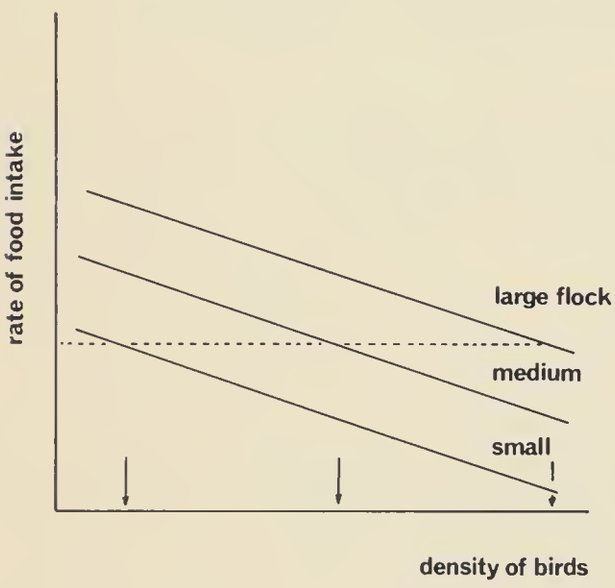

FIGURE 2. A graphical model to show how costs and benefits of flock feeding could interact to produce no difference in net benefit between birds in groups of different sizes (based on FRETWELL, 1972). There is a negative relationship between feeding rate and bird density, due to interference. The benefit of flocking is shown by three lines for the peck rate versus bird density relationship. At a given bird density it is better to be in a larger group, but at the densities indicated by the three arrows, peck rate is the same in large, medium and small flocks (dotted line).

Different individuals may benefit in different ways

Our second point can be summarised by saying that the frequency distribution of flock sizes could be an "evolutionarily stable strategy" in which the payoff to an individual is independent of flock size. The third, and perhaps most important point also uses an ESS argument. Studies similar to those summarised in Figure 1 have generally measured the average benefit to individuals in groups of different sizes. There are a few exceptions, for example MURTON (1971) has emphasised that subordinate Woodpigeons *Columba palumbus* in a flock may do worse than dominant individuals (see also

Caraco & Pulliam, this volume). Similarly, Barnard (1978) has shown that (presumed) subordinate birds in House Sparrow *Passer domesticus* flocks have a lower peck rate than dominants, and that they tend to stay behind in small groups when the rest of the flock leave a site. When they are left alone, their peck rate increases. Thus on average birds benefit from being in a flock (Fig. 1c), but very subordinate individuals may suffer.

We suggest that some of the most interesting consequences of flocking may be overlooked by measuring average benefits. Different individuals in a group may derive benefits in different ways. Suppose, for example, that some individuals in a flock (or species in a mixed flock) obtain most of their food by copying or kleptoparasitising while others are primarily searchers. It is intuitively easy to see that in a flock of pure searchers, a parasite will do well, but when parasites predominate, searching may be a more profitable option. It is possible to show graphically that there will be an evolutionarily stable mixture of the two strategies in which the benefits from searching or copying are equal. The stable mixture varies with flock size: as flock size increases the stable point contains a greater proportion of parasites (Sibly pers. comm.). Some qualitative support for these ideas comes from the work of Barnard (1978), who showed that in captive sparrow flocks, some individuals get most of their food by searching, while others are mainly copiers. These traits are probably to some extent flexible; individuals may adjust their strategy according to the proportion of the two individuals in a group. The benefit derived from copying increases with flock size and with the proportion of searchers in the group. It has not yet been possible to test in a quantitative way whether or not the hypothesised stable mixture is achieved, but this type of analysis will be only made possible by focussing on individual birds in a flock and measuring simultaneously structure, dynamics and benefits.

To summarise, our main points are that studies of the function of flocking should focus on differences between individuals rather than average values of benefit; they should seek to explain the structure and dynamics of flocks; and they should try to assess all the components of cost and benefit.

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Goose Flocks and Food Exploitation: How to Have your Cake and Eat It

Rudolf Drent

As reviewed elsewhere in this symposium (Krebs & Barnard) recent work on the adaptiveness of flocking centres on a food function as well as an antipredator function. Many observations argue for an enhancement of foraging in individuals making up the flock, by means of interchange of information, either during active foraging in the feeding areas or prior to departure from the night roost. In experiments with models we were able to show that when approaching potential foraging sites on their morning flight Barnacle Geese *Branta leucopsis* in winter are prone to land near groups of geese already on the ground, and moreover the attractiveness of the group already landed depends on what these birds are doing, specifically the proportion of grazing as distinct from alert birds. We feel that this indirect assessment of the foraging potential of feeding sites goes on between nearby flocks, and indeed within the flock as well, allowing a continual adjustment of the flock configuration and the path followed. Waves of alert behaviour precede shifts in site (either by flight or rapid walking) and may function in direct visual scanning of the alternative sites close by, including features of the vegetation as well as behaviour of nearby geese. In any case, a goose flock with a high proportion of birds on the alert (the birds stopping feeding to look about with extended neck) serves to mark a site lacking in some essential (freedom from disturbance in addition to food requirements). In a sense the individual birds making up a flock can be said to be "voting" on the suitability of the site, and casting a "no" with the alert will influence what the local group will do as well as giving an indication to geese in the vicinity. In the open habitats frequented by geese such signalling can be effective over considerable distances (by measuring the distance at which flocks in flight are deflected by models we estimate the maximal effective distance at roughly 500 m).

We will show that Barnacle and Brent *Branta bernicla* Geese habitually remove a very significant portion of the food plants available to them, that such intensive grazing yields benefits to the geese on the short term and possibly on the long term as well, and finally we will argue that this exploitation system depends on the flocking habit.

Goose flocks as a harvesting machine

The preferred feeding areas (polder) in our study area in the northern Netherlands attract heavy and consistent grazing pressures from year to year, suggesting that at least part of this wintering area has reached capacity. As the total population increases, more birds spill over into the surrounding saltmarsh. It is possible to estimate the intake of wild geese by means of droppings (the necessary steps include direct observation of the rate of dropping production in the vegetation studied, often in the range of 15—20 per hour; microscope analysis of the droppings to determine the plant species taken; determination of ash-free and sand-free weights of the droppings and relevant plant species for marker substances as calibrated in trials with captive individuals to

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determine digestibilities). The measurements of grazing pressure are thus conveniently done by counting droppings in permanent quadrats at fortnightly intervals, each dropping representing a certain amount of food removed. The major hurdle in most studies of grazing is the assessment of changes in the vegetation, more particularly the biomass changes of potential food sources. Fortunately, MILLER et al. (1973) have recently developed a scanner technique suitable for our scale of investigation whereby frequent light meter readings at two wavelengths (675 and 800 nm, corresponding to reflectance and absorption maxima respectively for chlorophyll) allow calculation of a chlorophyll index showing a reasonable correlation with standing green biomass as determined by clipping and hand sorting. If the data on grazing intensity (dropping counts) are now plotted against the biomass present it appears that both Barnacle and Brent Geese are highly sensitive to food stocks (Fig. 1). The simplest interpretation of the depletion rates depicted at the top (computed from the droppings counts converted by means of digestibility trials) is that below a lower threshold geese cannot exploit the vegetation (perhaps on account of declining bite size on short swards), and above an upper threshold the rate of removal plateaus, i. e. the geese cream off the same amount of living material.

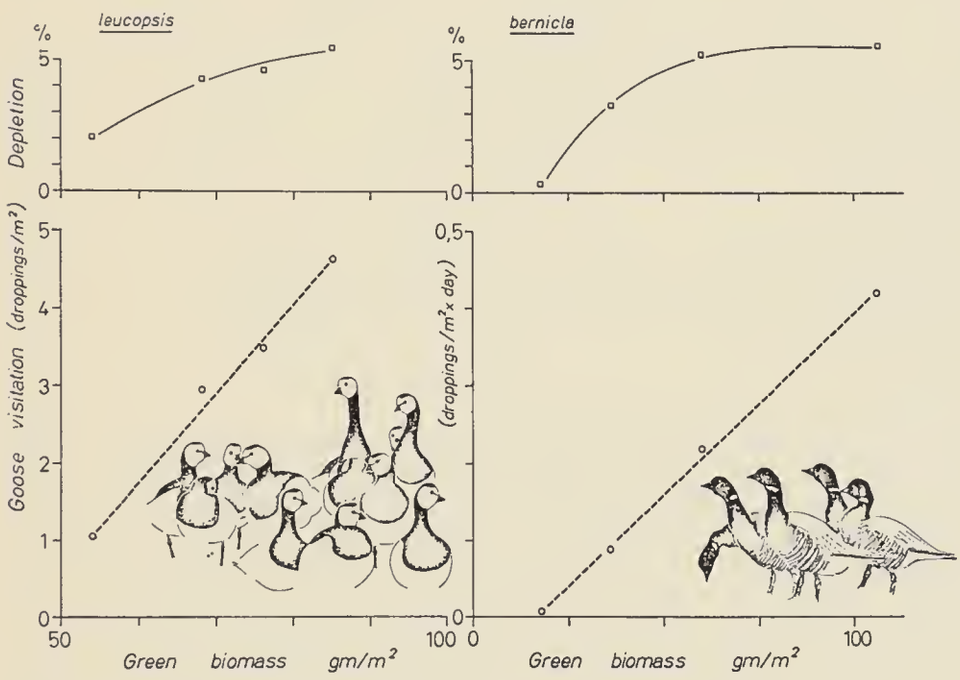

FIGURE 1. Data for the two *Branta* species showing that the birds graze areas with higher biomass more intensively.

We now ask what these seemingly modest rates of removal (approximately 5 % of the standing crop of living material during a three-week period) represent in terms of growth rates of the vegetation. Our most complete data concern the utilization of *Plantago maritima* by Brent in the course of May. At this time Brent double their food intake in order to finance the formation of fat depots sufficient to cover the cost of migration and survival during the egg phase when the then still inhospitable environment of the Siberian breeding grounds imposes a long period of starvation. In order to relate goose usage to vegetation growth in this period, a 30-hectare tract of salt marsh was kept under surveillance (from a raised observation tower 4m high) from dawn to

dusk continuously from 6 to 30 May 1978. By placing conspicuous stakes in a grid it was possible to record the visitation of the geese to individual hectare blocks, noting number of geese in each block every ten minutes and making spot checks on time budget (% foraging) scanning at least 100 birds. Little systematic variation in foraging percentage (generally between 85 % and 90 %) was noted, and the overall figures are presented here as total goose minutes per day. A striking periodicity of visitation is apparent (Fig. 2), and by scrutiny of the data on individual hectare blocks it was found that

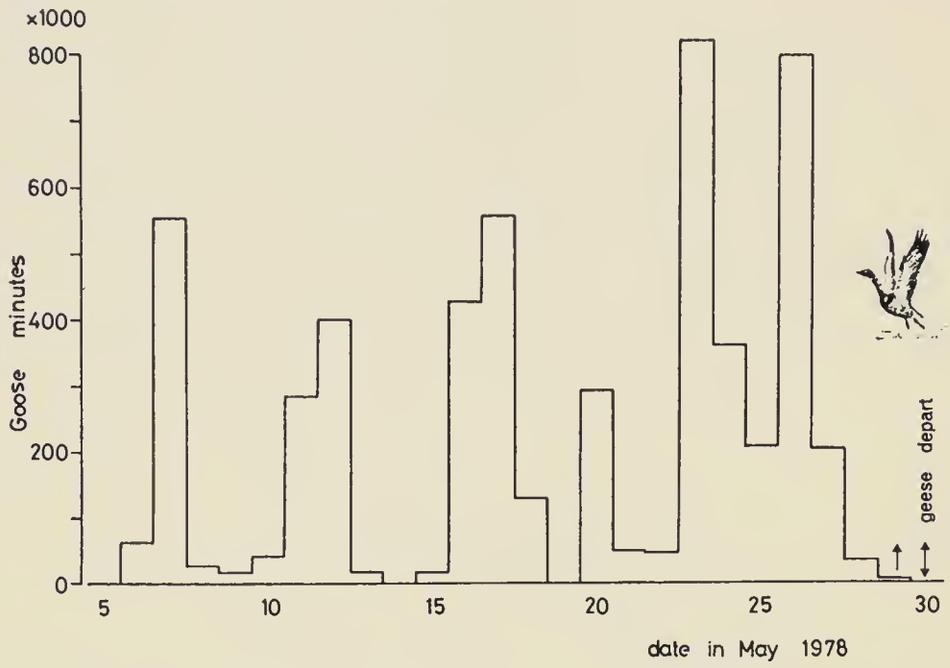

FIGURE 2. The pattern of visitation of Brent Geese to a 30-ha area of saltmarsh during 6—30 May 1978. The birds visit the plot about once every 4.7 days.

on average the geese made massive visits every 4.7 days (n = 42). (The definition of visit for these purposes is somewhat arbitrary, ignoring episodes accumulating less than 10 % of the minutes recorded on peak days.) By placing circular wire enclosures of 2m diameter, growth rates were estimated for vegetation released from goose grazing for periods of 5—10 days, the changes in biomass in the enclosures being followed by the lightmeter scanner method referred to earlier. Preliminary analysis of these data indicate that growth of *Plantago* at this site in 1978 was close to the long-term mean for this period of the year in a similar vegetation on the nearby island Terschelling. From

TABLE 1: A calculation to show that the geese crop nearly all the growth of *Plantago* which occurs between successive visits. The calculation involves the following steps: (a) The average interval between two visitations is 4.7 days (n = 42). (b) The growth of *Plantago* between visits is estimated by the lightmeter method described in the text. (c) The grazing intensity (in minutes) per metre^2 is estimated by direct observation (=7.1) and by droppings (=6.0) as 6.6 minutes. (d) The rate of food intake per minute is 0.3 g biomass, calculated from studies of captive geese. (e) The two measures (c) and (d) combined give the biomass removed per visit.

Interval between visitations:		4.7 days		
growth:	0,6 g biomass/day	× 4.7 days	= per interval	2.8 g
grazing duration per m^2:		6.6 minutes		
grass removed:	0.3 g biomass/minute	× 6.6 minutes	= per visit	2.0 g

digestibility trials carried out with captive birds on this vegetation we know what amount of food is taken per grazing minute, and as shown in Table 1 it appears that the goose flock removes a major part of the growth accumulated since the former visit. It is logical to postulate that the visitation frequency is determined by the growth rate of the plants, a recovery period allowing the individual grass blades to attain exploitable length being intercalated between visits. This argument hinges on the postulate that efficient foraging involves a fairly slow walking rate with attendant local exhaustion of the food supply.

The enhancement of growth rate by grazing is an established phenomenon, and we decided to see whether such could be demonstrated for Brent exploitation of *Plantago*. A clipping experiment reveals a growth optimum when approximately 30—50 % of the blade length is removed in a simulated goose visit (Fig. 3), and we were pleased to find

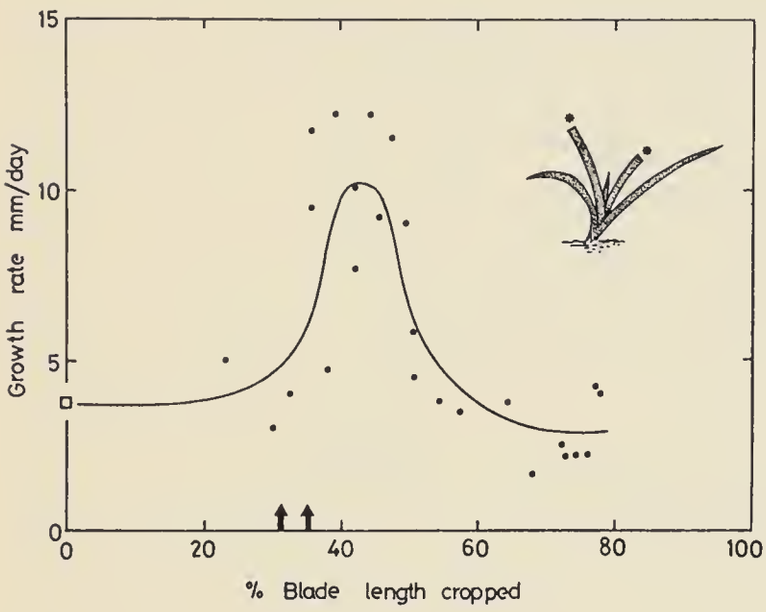

FIGURE 3. Clipping experiments show that *Plantago*, one of the major food plants on the saltmarsh, grows fastest when 30—50 % of the blade is removed. The geese remove about 35 % of the blade on a visit (shown by arrows).

that a reconstruction of a single goose visit indicates that the individual plants grazed suffer a 35 % decrement in total blade length, although of course not all plants in the sward are nibbled during each visit. The growth in the intervening 5 day interval is theoretically sufficient to allow renewed grazing of the same individual plant, but we have no evidence that this in fact occurs. A long-term effect of grazing concerns a stimulation of seed production, and it is possible that geese can exert a positive influence on their food plants by giving them a competitive edge, but a daunting amount of plant demography must be done to prove this. That the prolongation of growth through grazing involves a prolongation of the period of high protein content has been documented by HARWOOD (1977) for snow goose-vegetation interactions on the breeding grounds.

Limits to flock size

One of the hardest nuts to crack is the demonstration that there is a diminishing return to the individual as flock size increases above some optimum dictated by the quality, quantity, and configuration of the food stock. A hint that the depletion of local food stocks during a single goose flock visit is a reality emerges from an analysis of film material taken 22 May 1977. A cine-camera was mounted in a fixed position in the

observation tower on the same area studied in 1978, and frames were exposed at a speed of 4 per second as a goose flock moved through the area under view. The average grazing time per m^2 during this visit works out at 5 minutes, allowing the film material to be considered representative for what happens during one "massive visitation" as determined from observation and dropping counts immediately following (6.6 minutes grazing time per m^2, see Table 1). By calibrating the film subsequently by taking shots of a grid of stakes placed at meter intervals with the aid of a theodolite, we found that the resolution attained allows individual areas of 100 cm^2 to be distinguished. By spacing 50 such imaginary grazing plots evenly through the field of the negative, the fate of each could be followed by analysing the film frame by frame. In fact, more than three quarters of these plots were grazed in at least one frame of the film. As shown in Fig. 4, for plots visited 5 times or more a decrement in duration of

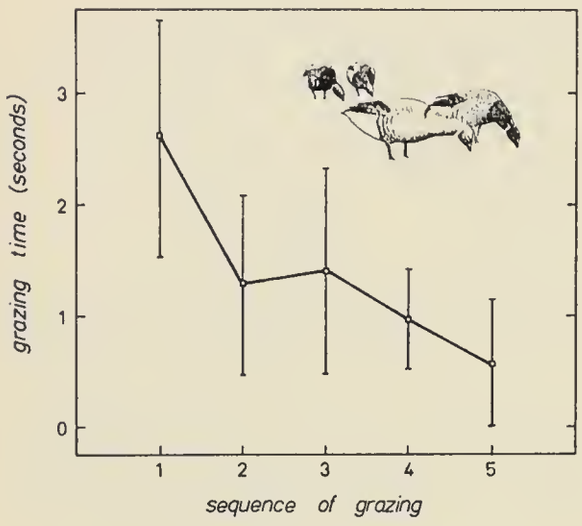

FIGURE 4. When a flock visits a area, individuals crossing a 100 cm^2 plot after five other geese have grazed the same place stay a shorter time than first-time visitors.

grazing as the flock moved over the area can be discerned, an effect not shown in plots visited only three times. If we assume that duration of grazing at one site is related to the food supply, two conclusions suggest themselves: (1) large local differences in food supply originally present, (2) a depletion of food supply at the better site during the visit, such that after the geese have passed through the whole area has been reduced to the same level. Since the last birds in the flock to reach the feeding sites thus face a deplenished food supply, and, possibly in consequence of this, spend a far higher proportion of the time on the alert and show an increased walking pace rate, dashing to keep up with the rest (VAN EERDEN, in prep.), we can speculate that flock limits can be set by weighing the advantage of depending on the local experience of birds already settled in the area against the penalty of lagging behind. We assume that social factors make it difficult for a newcomer to join the prime sector of the flock and detailed observation of individually recognizable Brent (colour rings allow recognition up to 300m) is underway to test this point.

Flocks as exploring parties

We have argued that grazing, at least in the spring, acts to enhance the food stock. First, grazing at the level observed stimulates the growth rate, and may as much as double it for short periods, and secondly on account of the systematic grazing coverage

attained by the geese the vegetation is maintained in a fresh leafy condition during a protracted period. Ungrazed swards rapidly become unpalatable to geese because of the accumulation of indigestible crude fibre components. Obviously early discovery of suitable food stocks carries a high premium.

How is the flock habit involved in this exploitation pattern? We have shown that in making a landing geese are highly sensitive to the actions of birds already on the ground, and we assume that the proportion of birds in the head-up alert posture, as well as the absolute size of the flock, gives an indication of foraging potential. Feeding groups in visual contact can also be thought of as interchanging information in this manner, thus pooling experience. The typical sequence is for flocks of 30—50 individuals to disperse over the feeding areas in the early morning, and within an hour or so most of these pioneering groups have shifted to join others so that loose flocks of 1500 or more coalesce and a large part of the day may be spent in this configuration. The salient features of this simultaneous sampling in the morning is that the individual groups can draw upon the findings of all other groups, thus quickly seeking out the exploitable sites as soon as they become available. But in another way, individual flocks can afford the extravagance of a foray into an unrewarding site, because they can profit from the discoveries of their neighbours — and geese as far away as 2—3 km may be considered neighbours. By contrast, in areas devoid of concentrations of food geese may forage as widely dispersed individual family parties, for example on the mudflats at low water when feeding on *Enteromorpha*.

Flocks reap the benefit of resource enhancement

From sightings of individually colour-ringed Brent from three observation towers spaced along the merse it has become clear that most birds confine their grazing to a relatively small area; the foraging units corresponding more or less to the areas within which all exploring parties coalesce in the feeding flock, in our situation roughly 2-km stretches of shoreline. We argue that all individuals are kept informed of developments in the area, participate in the first major grazing visit to a site as the spring growth appears, and will participate in the second and subsequent visits as growth permits. Put in another way, the flock habit not only avoids lost opportunities as argued above, but since flocks also have a certain operational zone on the island the flock members will themselves reap the benefit of increased yield and a protracted phase of succulent growth. This is a matter of interpretation, and poses the question of how geese manage to distribute themselves according to current food supplies, the critical event being the repulsion of large arrivals exceeding the local capacity. Intensive observation of marked birds seems the only avenue of approach to this problem.

The role of tradition in seeking out suitable feeding areas through the annual cycle is often stressed for geese, but the plasticity within the general pattern is impressive. Following the closure of the former Lauwerszee, an estuary that was completely cut off from the seas in 1969, a huge tract of *Salicornia* developed on what had been the tidal flats. The seeds of this plant provide a preferred food for the Barnacle Goose in the fall, and in fact the Lauwersmeer as it is now called harbours the entire Novaya Zembla population — some 50,000 individuals — in October, involving an impressive change in the migratory timetable, the geese advancing their date of arrival in the northern

Netherlands by upwards of three weeks (van Eerden & Prop, in prep.). As the salt is leached from the soil of this reclaimed area the *Salicornia* seed yield has started to decline, and it will be a spur to continued observation in the area to follow how the geese adjust to this change.

Further work

1. A further quantification of the short-term enhancement of the food supply by the grazing activities of geese is called for, and should include the growth stimulating effects of the release of phosphates from the droppings.

2. The long-term benefits to the geese, in tipping the competitive balance in favour of highly palatable species, for example by increasing seed yields as a response to grazing, should also be studied.

3. Gaining insight in how the geese distribute themselves in relation to the food supplies is the core problem, and besides passively watching seasonal shifts attempts should be made to alter the food supply. Fertilizer experiments are promising though one must be prepared for setbacks in a habitat that may be inundated unexpectedly, and mowing certain tracks in the evening prior to expected visitation might be particularly revealing. Manipulation of the food resource can be carried out to the greatest effect where a reasonable proportion of the geese have already been individually marked.

Acknowledgements

We wish to thank the Dienst der Domeinen for permission to work on the merse on Schiermonnikoog, and remember with gratitude the many services rendered by Mr. R. Niewenhuis and his staff on the island, transport of our cumbersome towers chief among them The continuous watch on the Brent in two spring seasons was possible through the combined efforts of T. Boudewijn, G. Eggink, M. Huisman, P. Oosterveld, H. Prins, Renske de Vries, Roelf de Vries and R. Ydenberg.

Time Budgets and Flocking Dynamics

Thomas Caraco

An extensive literature describes avian foraging flocks and interprets their significance. Some authors stress foraging efficiency hypotheses (e.g. Barash, 1974; Cody, 1971; Krebs, 1973, 1974), while others view flock feeding as incidental to an individual's protection from predation in a group (e. g. Hamilton, 1971; Siegfried & Underhill, 1975; Vine, 1971). More generally, flocking can be portrayed as an interactive response to factors governing survivorship and fecundity, where the benefits and costs of sociality may vary among individuals (Caraco, 1978; Powell, 1974; Pulliam, 1973, 1975; Treisman, 1975).

We have taken this interactive approach in our studies of granivorous winter flocks of Yellow-eyed Juncos *Junco phaeonotus*. The juncos exhibit a highly variable social system. Some days flock size does not exceed five birds, while under different conditions as many as 30 juncos may be seen feeding together.

An overwintering junco should seek to maximize its probability of surviving to the next breeding season. Survivorship depends on avoiding predation by accipiters and feeding sufficiently to avert starvation. Time constraints are extremely important in this system. Oxygen consumption and resource calorimetry studies (unpublished data) indicate that a junco must find and consume a seed every 8—12 seconds during the entire day at cold temperatures ($\leq 9°$ C.), in order to fulfill 24 hour energy requirements. However, foraging time cannot be expanded to the point where predator detection is inadequate. When a junco lifts its head to scan for a possible approaching predator, it momentarily ceases its search for food. Additionally, time is expended in aggression. Seed density is highly variable across our study area and sites of relatively high food availability are defended by dominant birds. Aggression can be advantageous to a dominant in a long-term sense, since fighting reduces flock size (individuals losing encounters often immediately depart the group). Therefore, aggression reduces the food depletion rate. Both the winner and loser of aggressive encounters lose foraging time. The immediate survivorship requirements of energy acquisition and predator detection limit the rate at which any junco can initiate aggression. Because of these constraints on the allocation of time, we have found that time budgets are the key to understanding the highly variable junco flocking system.

Yellow-eyed Junco time budgets depend on both flock size and environmental factors (Caraco, 1977; Pulliam et al., 1974). For a given set of ecological variables (discussed below), the proportions of time a junco expects to spend foraging, scanning for predators and engaged in aggression depend upon flock size. Since time budgets translate into the benefits and costs governing survivorship, we can predict the relative attractiveness of flocks of different sizes. Therefore, time budgeting patterns will influence flocking dynamics, the rates at which individuals join and depart flocks of differ-

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ent sizes. Knowledge of flocking dynamics predicts mean flock size, and can be employed to further estimate the statistical distribution of foraging group sizes (Caraco, 1978). We will describe the way time budgets vary with flock size, and then with four important environmental variables: temperature, food density, distance to cover where the juncos are safe from predators, and the presence of a predator in the immediate vicinity of foraging flocks. Thereafter, we discuss the response of arrival and departure rates to time budgeting differences, and explain how the flocking dynamics elucidate the highly variable flocking structure of Yellow-eyed Juncos.

Pulliam (1973) suggested that an advantage of flocking might be that an individual could scan for predators less often in a group, without a decrement in its probability of avoiding predation, and use the time gained to increase its feeding rate. Qualitative support for the hypothesis (e. g. Lazarus, 1972; Siegfried & Underhill, 1975) is available for several species, and Powell (1974) quantitatively verified the idea in an aviary experiment. Caraco's (1977) field study showed that individual Yellow-eyed Juncos decrease their rate of scanning for predators as flock size grows, and employ most of the time gained to increase their feeding rate at low and moderate levels of aggression. This group size dependent time budgeting would seem to make large flocks particularly attractive to subordinate juncos. However, larger flocks also mean that subordinates lose a greater proportion of time to aggression. Dominants initiate aggressive interactions more often in large flocks, since food is more quickly depleted as group size increases. Moreover, large flocks increase the probability of encounters within individual distances (Marler, 1956), so the group size dependent increase in aggression is not surprising.

When will subordinate juncos prefer membership in large flocks? For simplicity, assume that scanning rate variation, the probability of escaping an attack in different group sizes, and the conspicuousness of large flocks interact so that an individual junco has an equal and satisfactorily high probability of avoiding predation in any flock size. The mathematical complexity required without this assumption is detailed elsewhere (Caraco MS). Except for the dominant bird (or sometimes a male-female pair) defending a given feeding site's resources, juncos will favor large flocks whenever scanning time decreases faster with group size than time lost to aggression increases; i. e. whenever foraging time increases with flock size. Otherwise, small flocks provide faster energy acquisition.

Environmental variables determine the way foraging time and aggression change with flock size. On colder days an individual must spend more time foraging to meet daily energy expenditures and anticipated overnight costs. The requirement for predator watchfulness should be temperature independent. Foraging requirements on colder days result in dominants initiating fewer aggressive encounters, and individual distances decrease (Pulliam et al., 1974). Therefore, at low temperatures the time gained from reduced scanning exceeds increases in aggression as flock size grows, so that foraging time increases with the size of the flock. At warmer temperatures the increases in aggression more quickly surpass scanning time reductions with increasing flock size. At high temperatures, therefore, foraging time will begin to decrease at larger flock sizes, so that juncos will then prefer small feeding groups.

Food density also affects junco time butgets (Pulliam et al., 1974). Increased food density reduces the average search time per seed, allowing an individual to meet

24 hour caloric requirements with less time spent foraging. The reduction in required foraging time relaxes the time constraints on aggression, and dominants increase the rate at which they initiate aggressive encounters. We defer discussion of the impact of food desity on flock size until we consider flocking dynamics.

Yellow-eyed Juncos seldom forage far from cover, and fly to nearby bushes when a predator is sighted. However, if commercial grain is made available at high density far from cover, juncos will utilize the food. We monitored time budgets, flocking dynamics and group sizes at such a feeding station. We then placed a large bush in the midst of the seeds to provide cover and recorded similar data. Within group size, significantly more time is spent scanning for predators when cover is not available. The result seems reasonable in that an acceptable probability of avoiding predation should require earlier detection of a predator's approach as distance from cover increases. The greater scanning time without cover is accompanied by less time spent in both foraging and aggression (unpublished data). The experiment demonstrates the importance of available cover in determining a feeding site's attraction to juncos, independent of the site's food density.

Predator attack rate is another environmental variable that might influence junco time budgets. The frequency of predation observable in nature renders quantification of the impact of variable predation pressure an extremely long-term task. Therefore, we have experimentally introduced a trained Harris' Hawk *Parabuteo unicinctus,* with the aid of a falconer, and examined the juncos' response to a raptor's immediate presence. The hawk cannot capture a bird as quick and agile as a junco, but it follows its owner through the study area and can be directed to swoop down over junco flocks. The attack rate perceived by the juncos is greater than they normally face (cf. MORSE, 1973), but the experiment allows us to easily observe short-term time budgeting responses to the presence of a predator.

When the hawk is in the study area, juncos scan more often. Foraging and aggression, as well as total time on the ground, are reduced (unpublished data). Individual scanning rates are approximately 2.5 times greater with the hawk in the area. The hawk's presence has the same qualitative impact on time budgets as does lack of nearby cover.

Flocking dynamics

Since time budgets, and therefore the benefits and costs governing survivorship, vary with group size, we can expect the attractive and repulsive forces of different flocks sizes to vary. To examine the relationships of time budgeting to flocking dynamics and flock size characteristics, we define two arrival rate components and a departure rate. The first element of the arrival rate is the site quality response, i. e. the rate of arrival which is independent of flock size at a feeding site. We estimate site quality attraction by measuring the arrival rate at commonly utilized sites where no juncos are currently foraging (flock size is zero). This rate should increase as local food density increases and decrease if cover from predators is removed (CARACO, 1978). We have confirmed the second hypothesis (unpublished data). The food density response has been validated at high temperature, but does not appear to hold at relatively low temperature (CARACO, 1977). Further investigation of the interaction between temperature and a given feeding site's food density relative to other foraging areas is warranted.

The other element of the arrival rate is the response to flock size. When feeding rate increases with flock size, the arrival rate also increases with the size of the group. This will be the case at low temperatures, when the time constraints on aggression are maximal. As temperature and aggression increase, the feeding rate advantage in larger group sizes diminishes, and the arrival rate at any given flock size decreases. Increased food density also reduces the time constraints on aggression, and arrival rates again decrease (Caraco, 1977). Holding temperature and food density constant, the removal of cover from predators or the presence of a predator increases the arrival rate at most flock sizes, but juncos avoid very small flocks and solitary foraging at these times (unpublished data). These last two environmental conditions also dictate higher scanning rates and minimal aggression, so that relative feeding rates increase with flock size. If the probability of avoiding predation increases with flock size. (relaxing our previous assumption), large groups can be especially advantageous when cover is minimal or a predator is hunting in the area.

Departure rates depend on flock size, and Yellow-eyed Junco departure rates usually show a strong relationship to levels of aggression (Caraco, 1977). Aggression per individual increases with flock size, and departures often are immediately preceded by an aggressive interaction, with the loser being chased from the flock. Hence, departure rates always increase with flock size. Note that junco departure rates respond directly to aggression. Larger flocks show higher departure rates even when feeding rate increases with group size.

Since warmer temperatures and increased food density allow more aggression, the departure rate at any given junco flock size increases with both ambient temperature and seed density (Caraco, 1977). When cover is removed or a predator is present in the study area, departure rates are not so simply explained by aggression levels. Normally, juncos arrive and depart flocks independently (except when flushed to cover), so that each change in flock size is a statistically independent event. When cover is removed or a predator has been noticed in the study area, one bird's departure from a large flock is usually followed by the departure of several other juncos, even if the predator is not within sight of the flock. Such behavior is consistent with the increased wariness observed under these conditions, but cannot be predicted by the relatively low levels of aggression observed at such times.

How does variation in flocking dynamics affect the average junco flock size? Increasing temperature results in lower arrival rates and higher departure rates at any given group size. Therefore, mean group size (and group size variance) decreases as temperature rises (Caraco, 1978). Food density increments should, in theory, increase the site quality arrival rate component, decrease the group size dependent arrival rate component, and increase the departure rate at any flock size. Therefore, the change in mean group size should depend on the relative magnitudes of the responses in the three elements of the flocking dynamics. The junco site quality response to food density variation in our experiments has always been outweighed by the inverse relations between seed density and the group size dependent arrival rate. Therefore, increased food density results in smaller junco flock sizes (Caraco, 1977).

Removing cover has an interesting impact on mean flock size. During the experiment with high food density and no cover, small flocks were quite rare at the experi-

mental site, yet could be commonly found elsewhere in the study area. Generally, there were either no birds feeding at the experimental site or a large flock (10—20 birds) fed there. The site quality arrival rate was very low (as anticipated), so that both random and systematic sampling show many zeros and a low mean group size (unpublished data). If, however, sampling is conditional upon the presence of juncos at the site, there is a large mean group size. Juncos hesitate to use the experimental site, but once a few birds are present, high arrival rates quickly build up flock size. However, after a few departures occur, the rest of the flock flies quickly to cover. Similar behavior occurs with a predator in the study area. Social cohesion is high and aggression is minimal. Fewer flocks form, and these feeding groups are relatively large.

General comments

We expect the relationships among environmental factors affecting survivorship, time budgets and flocking dynamics will be applicable to most overwintering granivorous flocking species. An interesting comparison to the junco system may lie in flocks of winter migrants. One of us (HRP) has observed these feeding assemblages for several years. The interaction between physiological requirements, seed density and seed caloric value suggests that little time is available for activities other than those predicated by short-term survivorship requirements (wariness of predators and energy acquisition). The only common aggressive interactions are displacements at food clumps; dominance hierarchies do not form. We hope to demonstrate that the differences in time allocated to aggression explain (1) flocking dynamics comparisons between the juncos and the migrants, and (2) why migrant flocks are much larger than junco flocks.

The only other study of flocking dynamics is KREBS' (1974) work with Great Blue Herons *Ardea herodias*. That system is also time constrained, not by food size characteristics as in the juncos, but by the requirement to regularly deliver food to nestlings. The average rate at which fish are captured increases with flock size (to an asymptote), and the arrival rate also increases with flock size. Departures are not governed by aggression, but depend on the probability of a heron failing to make a prey capture within some critical time period. Flock size mirrors relative resource availability. Note that the response to food density is just the opposite to that observed in junco flocks. Junco food resources are economically defensible, so that aggression increases with food density. The temporal and spatial ephemerality of the herons' food does not favor resource defence. Therefore, sites of relatively high food density are characterized by relatively high arrival rates and low departure rates, resulting in a high mean flock size (KREBS, 1974).

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Mixed Species Flocking as a Strategy for Neotropical Residents

George V. N. Powell

Grouping by neotropical birds into mixed-species flocks is a widely occurring phenomenon that has attracted the attention of biologists for at least a century (Bates, 1863). However, in spite of this attention, there is still no consensus as to the role these groupings play in improving fitness. Two sets of hypotheses are commonly presented: grouping may improve foraging efficiency or it may reduce the probability of being captured by a predator.

In this paper I will briefly present data I collected during an intensive study of one type of multispecific association (Powell, 1977) and use these data to evaluate hypotheses that aim to explain the adaptive significance of grouping.

Multispecific associations of birds vary in size from a few to hundreds of members and in composition from resident to migrant associates. Generally, they are classified as either aggregations or flocks. Aggregations are groupings that incidentally form when individuals are drawn together by environmental factors. Typically, these are stationary resources such as fruiting trees, but the cues may be mobile as are army ant swarms or grass fires. True flocks are held together by social attraction between the birds. The diversity of multispecific groupings is an important consideration in the analysis of their adaptive significance because hypotheses applicable to one type of association may not be relevant to another. Aggregations forming at resource rich patches probably have a different purpose than flocks moving through a uniform environment. By the same token, flocks of migrants may serve a different function than flocks of winter residents.

The groups I studied were small mixed species flocks that commonly occur in forest understory throughout much of the new world tropics. The location of my intensive study was middle elevation forest in Costa Rica, Central America. Preparations for the study consisted of color marking the majority of understory residents on a forest tract of 11 ha and cutting a network of narrow paths that enabled me to unobtrusively follow birds through the understory. Concurrent with my study, Buskirk (1972) made a detailed analysis of the foraging behavior of the same group of birds. My discussion of foraging behavior is supported by these quantitative data.

Mixed species flocks on the study area were composed of small insectivorous species with diverse foraging habits, including foliage gleaning; stalk gleaning and probing; rummaging, i. e. searching through detritus and epiphytes; terrestrial foraging; and limited amounts of flycatching. Several species augmented their diet with fruit. Buskirk's analysis of foraging behavior, which was based on measurements of 7 foraging parameters, indicates that these species have little overlap in food resources. Eleven neotropical species accounted for 90 % of the individuals in flocks (Table 1). One of these, *Basileuterus tristriatus,* was the nucleus around which flocks formed. The presence of this species was a prerequisite for the formation of mixed flocks in the understory. In addition to these eleven species, approximately thirty additional species joined

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TABLE 1: Foraging behavior and characteristics of flock participation of species that formed mixed species flocks in the understory of the study area. Foraging behavior, terms and abbreviations as follows:—Aerial, insects captured from the air; Foliage, arthropods gleaned from foliage and branchlets; Ground, arthropods and plant materials obtained from on the ground; Rummage, search through detritus and epiphytes for arthropods; Probe, arthropods taken from surfaces of trunks and major branches, T, or smaller stems and branches, S; Veg, feed on reproductive parts of plants.

Species	Foraging Behavior	Frequency of Association (%)	Area of Home Range ha (n)
Basileuterus tristriatus	Foliage	100	4.7
Premnoplex brunnescens	Probe (S)	75	2.9 (1)
Henicorhina leucophrys	Rummage (S)	44	0.7 (6)
Basileuterus culicivorus	Foliage	34	4.1 (1)
Atlapetes brunneinucha	Ground	26.4	0.8 (2)
Chlorospingus ophthalmicus	Veg-Rummage	20.2	0.5 (6)
Myioborus miniatus	Aerial	19.2	0.8 (3)
Syndactyla subalaris	Rummage (T&S)	17.5	2.6 (1)
Cranioleuca erythrops	Rummage (S)	13.6	2.4 (1)
Xiphorhynchus erythropygius	Probe (T)	13.2	3.0 (1)
Sittasomus griseicapillus	Probe (T)	11.7	3.5 (1)

the flocks infrequently. A few were seasonal migrants from the temperate zone, some bred locally, but not on the study area, and the remainder are common in the area but infrequently joined flocks.

Understory mixed flocks are constantly changing associations that move through the forest on courses that frequently cross but rarely retrace previous paths. A comparison of flock movements with computer simulations of bounded random walks indicates that flocks return to areas they have previously exploited at a higher frequency than expected. Analysis of movement patterns also reveals that flocks decrease the frequency of site revisitation during periods of reduced food availability. The use of space by the flocks is sufficiently uniform to indicate that the distribution of food is fairly homogeneous. Data collected from four consecutive complete days of following one flock in each of three months indicate that flocks neither linger in nor return frequently to any parts of their home ranges. There is no correlation in movement rates recorded in successive short time intervals, which indicates that flocks do not exhibit a pattern of moving rapidly between and slowly within resource patches.

Data from color-ringed individuals reveal that flock participants are part of a stable community inhabiting the forest understory. Species that are consistent flock participants mate for life and are territorial year round, even though they breed only 5 months of the year. Territories vary in size from half to four ha (Table 1). Superimposing one species' territories on another reveals that each species divides the habitat independently of the others. Individuals are restricted to following flocks that are in their territories. When a flock leaves the territory of one of its members, the member generally drops from the flock and the neighboring conspecific whose territory has just been entered may join. Territory boundaries account for 65 % of turnover in flock composition. The likelihood that a resident will join a mixed flock is directly propor-

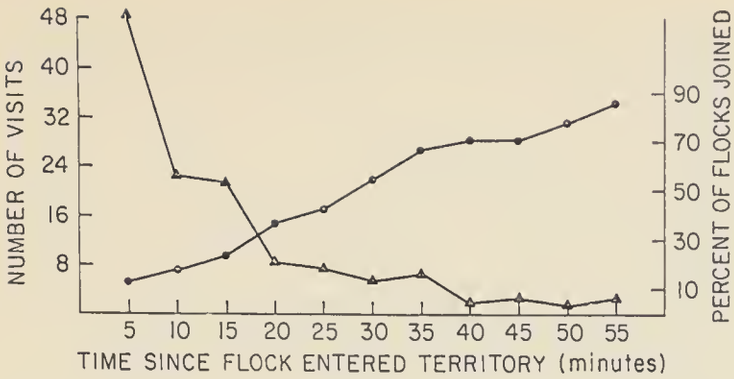

Figure 1. The length of time that the mixed species flock remained in territories of attendants (▲), and the likelihood that residents joined the mixed flock (●), $y = 1.5x - 1.0$; $r = .9$.

tional to the time the flock is in its territory (Fig. 1). The time taken by the resident to join a flock appears to be an expression both of the time it takes an individual to discover the flock in its territory and the costs and benefits of joining the flock after it is discovered. Cost-benefit ratios may be influenced by whether or not a conspecific is with the flock. As mentioned earlier, followers leave the flock at their respective boundaries but sometimes, in the absence of a neighbor, they trespass. If they are discovered, a fight ensues until the trespasser retreats. Residents that approach a flock to drive out trespassers are more likely to join the flock. There is both an annual and a daily cycle in flocking propensities. Flocks are smallest in the breeding season, a restricted period of five months when all of the common flock participants reproduce. Flock size during the nonbreeding season was inversely proportional to relative arthropod density as measured by volume and number of arthropods captured in Malaise traps on the study area (Fig. 2).

In summary, color-marking and following mixed species flocks has shown that what appeared to be a random assortment of birds is actually an organized community restricted to relatively few individuals. Because of territoriality, mixed flocks contain only a single pair of each species and flock size is correlated with number of species that join and not the number of individuals of each species. Seasonal increases in average flock size do not result from new birds migrating into the area. Instead, size fluctuations result from changes in flocking propensities of individuals that are present all year round. Since the nuclear species of mixed flocks is territorial, only one pair of nuclear species coincides with the territory of each resident flock participant. Therefore, only one mixed species flock is available to most flock participants. If they fail to join the flock when it is accessible, they can join no other. Thus birds that are absent from a flock during the time it is in their territories are not flocking elsewhere.

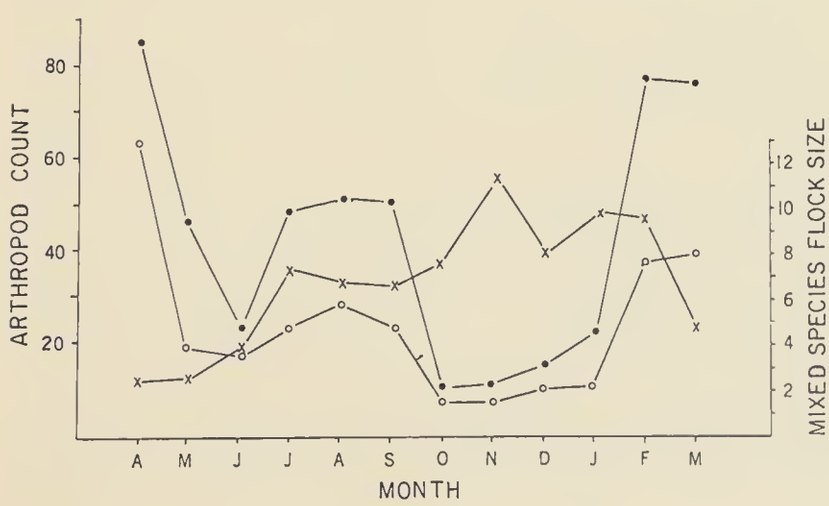

Figure 2. Mean daily volume and number of insects captured in a Malaise trap on the study area (from Powell, in prep.) and mean size (number of individuals) of mixed species flocks. Symbols: number of insects, ●; volume of insects (ml × 10), ○: and flock size, X.

With this brief overview, I would like to run through the various hypotheses that are considered as possible advantages for grouping.

Foraging enhancement hypotheses

Disturbance created by flock members flushes cryptic insects making them easier to capture (Belt, 1874).

Characteristics of these mixed flocks make them poorly organized to capitalize on the beater effect. Nearest neighbor distance of flock participants is 2—3 m (Buskirk, 1972), and birds rarely forage over substrate that has been visited by other flock members. Thus, participants could only benefit from beaters that actually cause invertebrates to fly or drop considerable distances. However, aerial capture and pursuit of dislodged prey constitute only 8 % of feeding maneuvers in these flocks (Buskirk, 1972). Actually, the warbler which relies most heavily on aerial captures, *Myioborus miniatus*, decreases its reliance on this form of foraging while in flocks. Finally, three common species that capitalize on the beater effect by feeding on insects that are flushed by army ant swarms rarely associate with mixed flocks, even when no ant swarms are available. These species should be logical benefactors if the beater effect were operative with mixed flocks.

Flocking is a means of transferring awareness of new of concentrated food sources (Ward, 1965).

Permanent territoriality of resident mixed flock participants weakens the applicability of information transfer hypotheses. Since flock attendants are restricted to home ranges averaging 2 hectares, they will maintain a high degree of familiarity with food resource distribution. Residents are unlikely to gain new information about food resources by following mixed flocks. Since residents exclude all conspecifics from their territories, intraspecitic transfer of information is prevented. Juveniles and floaters, classes with the greatest potential for gaining from information transfer, are excluded from mixed flocks. Information regarding new types of food may be interspecifically transferable among territorial residents. However, as I mentioned earlier, participants occupy diverse foraging niches with little overlap in the use of feeding substrates. Therefore, it seems unlikely that information about new food resources for one species would be relevant to other participating species.

Mixed species flock participants with similar feeding ecology lessen competition either by reducing niche (Morse, 1967) or spatial overlap (Miller, 1922).

Reduction of niche overlap is dependent on reciprocal reduction in breadth of foraging behavior. It implies that the dominant members of dyads or triads with overlapping foraging niches gain more by abandoning portions of their foraging substrate or repertoire than by agonistically excluding subordinates from the zone of overlap. However, this hypothesis does not explain why residents associate in mixed flocks, since niche modification could be accomplished independently of flocks. The high stability of the understory community eliminates the need for residents to use mixed flocks to monitor local density of species with overlapping foraging habits. Furthermore, food niche

overlap among resident mixed flock participants increases when in a flock rather than decreases as predicted by this hypothesis. There is a significant reduction in foraging height diversity, and a shift towards foliage gleaning.

The second part of the overlap reduction hypothesis predicts that individuals join mixed flocks, monitor locations used and subsequently avoid those sites (Cody, 1971). Areas cropped by a flock are avoided until food resources are restored or redistributed. Mixed flocks of territorial residents present problems for this hypothesis. Intraspecific overlap cannot be decreased by flocking since participating species forage in pairs, or pairs with young, irrespective of their affiliation with mixed flocks. In fact, following flocks may increase intraspecific overlap. The constraints of permanent territoriality limit most birds to following flocks for 20 to 50 percent of their active periods. The rest of the time no flock is present for them to join. To efficiently use available space, territorial residents must adopt movement patterns that minimize self overlap independent of flocks. Since the flock visits are unpredictable, they are not likely to be compatible with residents' independent usage patterns. Consequently, following flocks frequently results in revisitation of areas previously visited in their absence. The potential for reducing interspecific overlap is minor since foraging behavior is so diverse. Species infrequently forage on substrate used by others, and if they do, they are usually searching for different types of organisms.

Predation avoidance hypotheses

Most observations of raptors preying on small birds indicate that early detection of predators is an effective means of avoiding predation (Tinbergen, 1946; Rudebeck, 1950, 1951; Markgren, 1960; Bengtson, 1971; Morse, 1973; Schipper et al., 1975).

The physiognomy of understory habitat, and the behavior of birds inhabiting it suggest that predation plays an important role in the evolution of resident mixed flocks. While following flocks, I regularly observed non-predators, often flock members, make rapid flights that caused other members to give brief warning calls and fly or drop to cover. Frequently, other species responded to the warning calls by interrupting foraging and reconnoitring their surroundings. When actual predatory attacks occurred, the warning calls were prolonged and all flock members fled to cover.

Flocking increases the effectiveness of surveillance against attack from predators beyond that possible for a single bird (Bates, 1863).

Surveillance can be enhanced either by increasing the number of sensory receptors or by delegating a sentinel. In a literal sense sentinels have not been observed in mixed flocks. However, species vary in their capacities to maintain awareness while foraging, so it is possible that less efficient surveillants, particularly stalk probers and gleaners, gain awareness by joining mixed flocks. In the flocks I observed, two species that comprised 15 % of flocks initiated three quarters of mobbing episodes. The enhancement of surveillance through addition of flock members, the "many eyes" hypothesis, has been demonstrated theoretically and experimentally. Flocks of European Starlings held in large cages responded more quickly than single birds to an approaching hawk model (Powell, 1974). In two of four predator attacks that I witnessed while following mixed flocks, the intended prey avoided probable capture by responding to warning notes

given by other flock members. Positioning in these attacks made it unlikely that the indended prey observed the attacking predator prior to escaping.

Predators experience difficulty attacking grouped individuals.

Flocks may reduce predatory attacks by confounding selection of specific prey or by presenting the threat of physical damage from collision with other flock members. These hypotheses have limited application to small mixed flocks since their size is probably insufficient to cause either confusion or increased risk of collision between predator and fleeing flock members. Because of the high species diversity in mixed flocks, most individuals look distinct so predators should have little difficulty selecting and chasing specific flock members. The potential for inflicting damage is probably minor since flock members scatter rather than clump when attacked. Understory avian predators' reliance on quick maneuverability further minimizes the threat of collision.

Conclusions

Attempts to assess the relative importance of flocking hypotheses have generally proven unsatisfactory. In part, this is because analyses have tended to consider flocks as a monolithic form of social behavior. It is probable that different types of flocks have evolved in response to different selective pressures and that mixed flocks of permanent residents that engage in year round territoriality serve different functions than fluid flocks of transient birds. Therefore, it is necessary to determine the relative importance of improving foraging efficiency or predation evasion for a specific flocking system. This problem is complicated by the fact that efficient foraging and predation evasion are interdependent. Increased protection against predation allows more efficient foraging and vice versa. This relationship was demonstrated experimentally with increasing group sizes of caged Starlings which both responded more quickly to a predator model and foraged more efficiently.

Organizational characteristics of permanent territorial residents that make up resident flocks minimize the applicability of the foraging efficiency hypotheses. Intraspecific group size is the same in and out of flocks so there is no potential for reducing intraspecific overlap. Formation of mixed flocks does not appear to reduce competition for food resources. Food niche overlap is minimal among participants and convergence of foraging behavior is exhibited when birds join. Visitation and foraging rate data are suggestive of relatively uniform food resource distribution, and wide separation and diverse foraging habits minimize potential for information sharing. In contrast, the flocks occupy an environment very favorable to avian predators that are common inhabitants of the study area forest. Flocks respond with effective integrated predator avoidance behavior when potentially threatened, and observations of predation attempts on flocks suggest that reducing the potential for surprise is an effective means of reducing predator success.

Thus, circumstantial evidence implicates predation pressures as a principal force behind mixed flock formation by permanent residents. However, the correlation between monthly mean flock size and relative density of arthropods suggests that food availability influences flocking behavior. The need for intensified foraging during periods of low food availability may increase vulnerability to predation. This would favor

associating with species that do not compete for scarce food resources, but have compatible movement patterns. Therefore, tropical residents can have their cake and eat it too. They form mixed species flocks and continue to exclude floating conspecifics. The delicacy of the balance between benefits and costs of flocking is indicated by the low propensity of residents to join flocks that are not in the immediate vicinity even though they may be in the residents' territories. Apparently in the absence of trespassers, the costs of interrupting foraging and moving to the flock or possibly the need to modify foraging behavior while flocking outweigh the benefits of joining. This level of precision in the balance of parameters makes it exceedingly difficult to discriminate among hypotheses on a quantitative basis. It is unlikely that we will reach beyond the subjective level for some time to come.

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SYMPOSIUM ON
BIOLOGICAL SIGNIFICANCE OF PAIR-BOND

11. VI. 1978

CONVENER: W. WICKLER

Coulson, J. C.: A Study of the Factors Influencing the Duration of the Pair-Bond in the Kittiwake Gull *Rissa tridactyla* 823

A Study of the Factors Influencing the Duration of the Pair-Bond in the Kittiwake Gull *Rissa tridactyla*

J. C. Coulson

Introduction

This investigation is based entirely upon field observation of one colony of the Kittiwake *Rissa tridactyla* at North Shields, England, where each breeding adult is individually colour-marked. The results presented in this paper were obtained in 25 consecutive breeding seasons between 1954 and 1978 during which time the colony progressively grew to about 100 breeding pairs. As a result of this study, large samples are available which allow several variables to be analysed simultaneously.

The discrete nature of the nest-site in the Kittiwake allows change of nest-site to be easily determined, whilst the return of all surviving birds to the same colony facilitates the calculation of annual mortality rates and the nature of the change or re-establishment of the pair-bond in successive years.

Previously, it has been shown that Kittiwakes which retain their mate from one breeding season to the next lay more eggs, incubate and rear their young better and fledge significantly more young than do birds which are in all other respects similar but are forming the particular pair-bond for the first time (Coulson 1972). Further, it was established that there was a positive correlation between unsuccessful breeding in one year and the probability of changing mate in the next breeding season. Evidence was presented to suggest that failure to breed successfully was often caused by a degree of "incompatibility" between the members of the pair. The observed situation accorded closely with that which would be expected on the basis of natural selection theory; the successful pairs remained together and become more successful and the failed breeders chose new mates which tended to make them, on average, more successful than they would have been with their previous mate.

This investigation extends the study and explores in more detail the factors which are linked with changes in the pair-bond. In addition a hypothesis is advanced to explain the mechanism of changing of mate ("divorce") when both members of a pair survive from one year to the next but take different mates, and of maintaining the pair-bond in successive years.

Definition of terms

Since many of the Kittiwakes involved in this study were not marked until they bred for the first time, their precise age is not known in many cases. Wooller & Coulson (1977) have shown that most Kittiwakes breed for the first time when 3 or 4 years old. Throughout this paper the term "age" has been used to denote the number of years in which the bird had bred and therefore underestimates in true age by 3 or 4 years. This

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is comparable with "previous breeding experience" used in earlier papers on Kittiwakes.

The colony has been divided into two areas, "centre" and "edge" since the breeding performance of birds nesting in these areas has been shown to differ (Coulson 1968, Wooller & Coulson 1977). Although these terms give a fairly precise description of the division, the separation has been made by selecting those nest sites as belonging to the "centre" which were occupied when the colony was only half its ultimate size.

Once a pair of Kittiwakes have bred together, the pair-bond may be re-established in the next breeding season ("same mate"). Alternatively, the pair-bond from the previous year may not be re-established and this can occur in two ways. First, one of the partners may have died in the intervening period ("dead"), or, secondly, the members of the pair may have both survived and returned to the colony but have selected different mates ("divorce"). We have no records of breeding Kittiwakes moving to a different colony although extensive searches have been made (Coulson & Wooller, 1976) and this method of causing a change in the pair bond does not normally exist in this species.

Duration of the pair-bond

The duration of the pair-bond in the Kittiwakes in our study colony has ranged from one to 14 consecutive years. Figure 1 shows the duration of all pair-bonds in the colony which were formed before 1969. Over half of all of the pair-bonds lasted one breeding season only. For the past 10 years, the data fit well to a simple model where half of the existing pair-bonds break up each year. After ten years, there are appreciably more long established pair-bonds than would be expected (one lasting 14 years would be

Figure 1. The duration of pair bonds (in years) in Kittiwake pairs formed before 1969. The results are expressed as a percentage of the total number of pairs considered. Note the decay curve suggesting that about half of the pair bonds break up each year.

expected to occur only about once in a half million pairs). Such a model of divorce is too simple since it is known that both adult mortality and the divorce rate change considerably with the age of the birds (see below), and any consistency in the pattern in the first ten years is due to the compensation of one variable by the other.

Age of members of the pair

Table 1 shows the age of male and female Kittiwakes forming all pairs in the colony in each year. There is a wide range of differences in the age of the partners (Fig. 2) although there is a tendency for the mate to be of the same or similar age, particularly amongst the younger birds. This table is composed of many records of the same pair of birds which have retained the same mate in successive years and this tends to emphasize the similar age effect. Table 2 includes the pair only in the year the pair-bond is formed for the first time and here a rather different picture emerges. Older birds of both sexes tend to take younger birds as their mate and no attempt is made by older birds to pair with birds of similar age and breeding experience.

The mean age of the new mates of mates of males and females in each year class is presented in Fig. 3. This clearly shows that both sexes tend to select younger mates as they become older and amongst the oldest birds of both sexes, the mean age of their mates is actually lower than the mates of those between 7 and 9 years. This selection of

TABLE 1. The age of the members of each pair in each year of the study. The diagonal lines enclose the birds of the same age (breeding experience).

Age male \ Age female	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
18					1														
17				1															
16	1		1																
15	1	1							1						1				
14	1							1	1			1	1	1					
13						1	3	2		1	1	2	1		1				
12		1				2	3	1	1	1	2	2	1	2					
11	2		2	1	3		1	3	1	2	2	2	2		1	2			
10	1	2	1	4		2	5	1	4	7	2	3		1	4				
9	2	2	2	2	2	7	2	6	9	2	3		2	4		1	1		
8	2	2	3	4	8	2	9	11	1	5		2	2		1	1			
7	3	4	4	7	6	13	17	5	4	2	4	4	3	1	1				
6	6	5	8	10	17	20	6	5	3	7	3	4	1	1	1				
5	11	13	13	17	23	13	8	3	7	2	4	1	4	1	1				
4	17	19	26	37	15	11	6	10	4	5	2	3	1	1				1	
3	25	27	55	20	15	11	13	8	8	6	6	3	1		1		2		
2	45	74	32	19	16	15	6	5	6	2	3	2	1	1		1	1		
1	191	44	28	21	20	7	6	11	2	3	3		1	3		2		1	

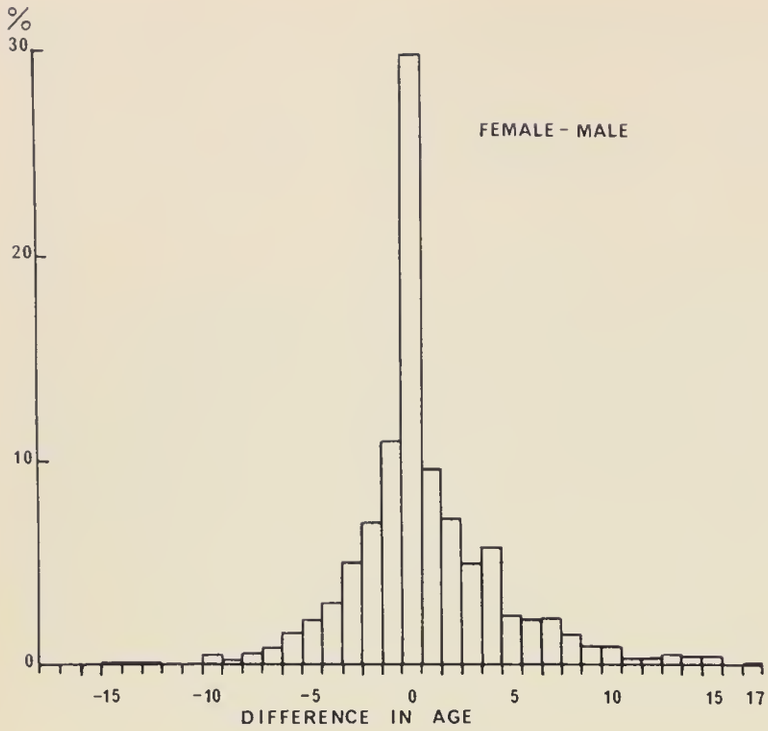

FIGURE 2. The difference in age (expressed as years of breeding experience) of the male and female members of a pair. About 30 % of the pairs have the same breeding experience. The difference in the distributions on each side of the mode is caused by the difference in survival rates of male and female Kittiwakes.

pairs with widely different age and breeding experience is of considerable interest in elucidating the roles of male and female age in determining breeding success.

The sources of new mates for birds which have already bred on at least one previous occasion is given in Table 3. There is a similar tendency for both males and females to

TABLE 2. The age of the members of each pair in the first year that they bred together. The diagonal lines enclose the birds of the same age (breeding experience).

Age male \ Age female	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
16	1																		
15	1																		
14	1																		
13						1	1	1											
12		1				1	3												
11	2		1	1	1														
10	1	1		4		1	1								1				
9	2	2		1		1			2					1					
8	2	1	2	4	4	2	1			1						1			
7	3	3	4	4	2	7	2	2				1	1						
6	6	3	3	5	6	4		1	2	2		1							
5	11	7	7	6	3	4	5	2	2			1	1		1				
4	17	13	13	7	3	6	3	4	1		2	1	1	1					
3	25	7	16	8	6	4	6	4	5	2	3	2					1		
2	45	23	13	8	6	10	4	4	1	2		1	1			1			
1	191	44	28	21	20	7	6	11	2	3	3		1	3		2		1	

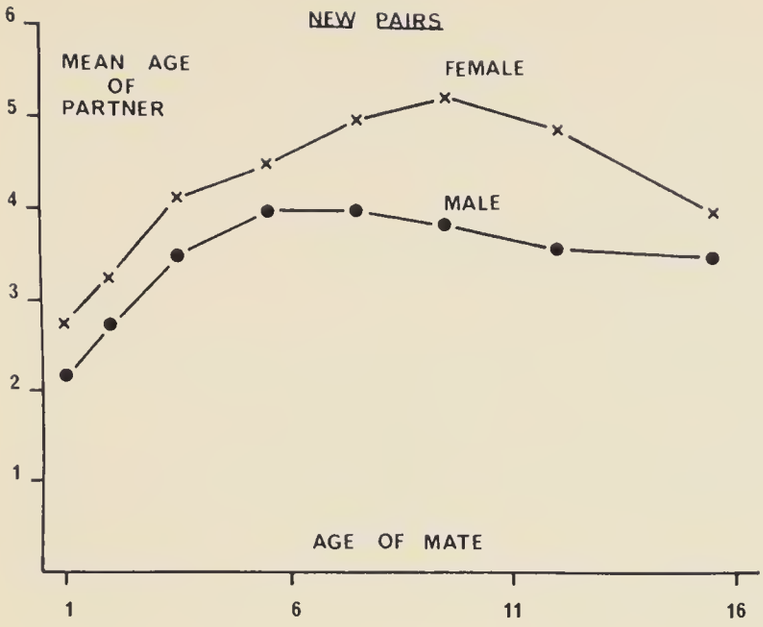

Figure 3. The mean age of partners of birds in different age groups. Crosses denote the mean age of females paired with males of given ages. Solid circles denote the mean age of males paired with females of given ages. Note the difference in the two curves (caused by the higher survival rates of females) and the trend in boths sexes for old birds to take younger mates than middle-aged birds.

pair with birds which have missed a breeding season (12 % and 13 %) and which have been divorced (41 % and 39 %). However there are appreciable differences between the two sexes in the selection as mates of birds which have not bred before. This is caused by the higher adult mortality rate of the males. Males took as new mates almost twice as many females which have lost their previous mate through mortality than females took widowed males.

Table 3. The sources of a new mate for male and female kittiwakes which have already bred

new mate	male	female
bird which has not bred before	25 %	37 %
bird which missed breeding last year	12 %	13 %
bird whose previous mate had died	22 %	12 %
bird which has divorced previous mate	41 %	39 %
total sample	358	300

Factors influencing the length of the pair-bond

The break up of a previous pair-bond is brought about by two causes, the mortality rate of the breeding birds and by the divorce of surviving pairs.

Factors affecting the survival rate

Recently Coulson & Wooller (1977) have made a detailed analysis of the survival rate of the Kittiwake. Clearly, the higher the survival rate, the greater opportunity there is that a previous pair will reform and maintain a pair-bond which existed in the previous year. Essentially, the following factors have been established which influence survival rates in the Kittiwake.

Age. The survival rate of both male and female Kittiwakes decreases with age (Fig. 4).

Sex. The survival rate of males is lower than that of females of the same age. In older age classes the mortality rate is double that of young breeding birds.

Position in the colony. During the growth phase of the study colony, the survival rates of birds nesting centrally in the colony was significantly greater than those at the edge although no predation occurred at the colony. Once the colony reached a stable size, the differential mortality decreased and, on existing data, is not significant.

Time. During the study on the colony, the survival rate of the Kittiwakes breeding has progressively decreased. In part this is due to the increased age distribution once the population has reached stability but there has also been a progressively slower survival rate amongst birds of comparable age. The cause of this change has not been identified, but is apparently not due to pesticides and is being investigated further. Two main possibilities are being considered. First, that this is an effect of the change in the structure of the colony and reflects greater "stress" in the larger colony or secondly, it is part of a more extensive decrease in survival affecting a large geographical area.

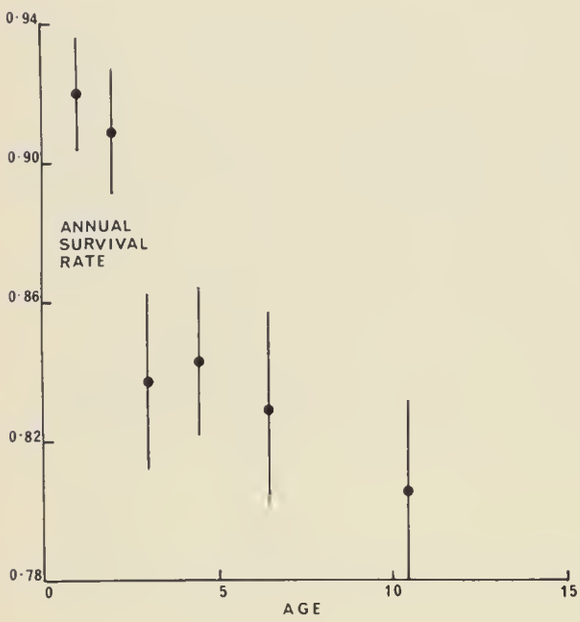

FIGURE 4. The annual survival rates of female Kittiwakes in relation to their age. The vertical lines indicate the range of one standard error of each survival rate. Note the tendency for the survival rate to decrease with age; a similar relationship exists in the male.

Factors influencing the duration of the pair-bond

Age. The divorce rate, calculated only from those pairs which survived from one breeding season to the next, declines with the age of the female (Fig. 5) and also with the age of the male. In general, the data are consistent with the suggestion that there is a steady and progressive decrease with age although there appears to be a marked "step" in the divorce rate between 7 and 8 years. Thus the similar annual rate of change of mates between pair-bonds lasting 1 to 10 years already referred to, is as a result of two complementary factors. As age increases there is a change from the importance of divorce to the dominance of the male mortality rate in causing the break in a pair-bond (Fig. 6).

Length of existing pair-bond. Birds of similar age are more likely to divorce their mate if their existing pair-bond is a new one. The results and analysis of the effects of age and the duration of the pair-bond on the divorce rate are given in Table 4. Apart from the obvious age effect already described, it is also evident that a pair-bond which has remained unchanged through two breeding seasons is much less likely

TABLE 4. The relationship between age, duration of the pair bond and the probability of divorce

probality of divorce next year							
pair first formed	female breeding age now						
	1	2	3	4 and 5	6 and 7	8 to 11	12 to 18
this year	0.39	0.41	0.43	0.30	0.32	0.21	0.25
last year	—	0.23	0.33	0.33	0.23	0.07	0.00
two or more years ago	—	—	0.11	0.24	0.09	0.10	0.00
sample sizes							
pair first formed							
this year	152	70	47	67	48	47	12
last year	0	52	24	45	26	31	5
two or more years ago	0	0	28	64	43	69	28

to result in a divorce in the next breeding season than in a pair formed in the current breeding season. This effect appears to become more pronounced in older birds. Similarly, there is a strong indication that the risk of divorce is even less in the pairs where the pair-bond has persisted for more than 2 breeding seasons (Table 4). Although the divorce rate is about 40 % in young birds with new mates, no cases of divorce were recorded in 33 pairs where the female had already bred for more than 11 years and where the pair-bond had existed for at least two breeding seasons. Clearly the combined effect of age and a lasting pair-bond has a marked effect on the divorce rate in the Kittiwake.

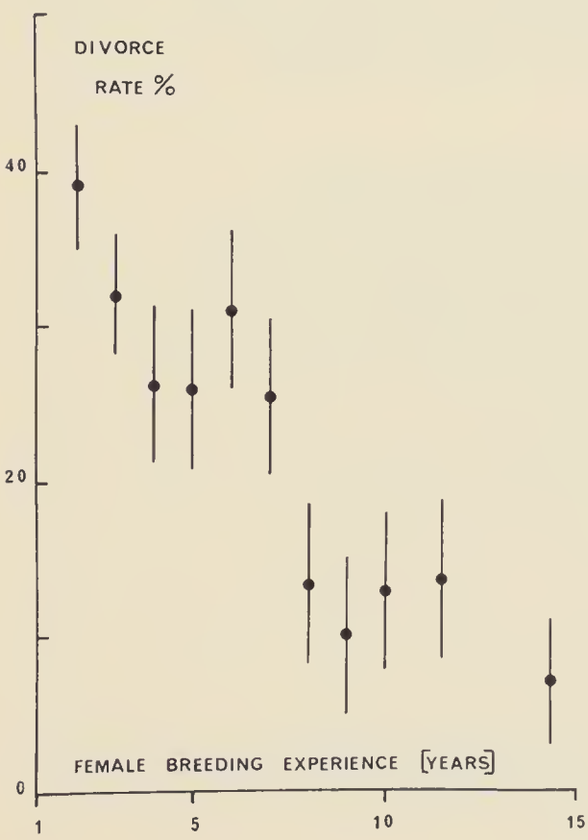

FIGURE 5. The divorce rate of female Kittiwakes in relation to their breeding age. The vertical lines indicate the range of one standard error. Note the progressive decrease in divorce rate with increased age.

The relationship between the annual divorce rate and the annual adult mortality rate. In years when the adult mortality rates are higher than average, fewer pairs survive to be at risk to divorce. Nevertheless, in such years there are more birds in search of a new mate and it is possible that this could have an effect on the divorce rate. The correlation between the annual mortality rate and annual divorce rate for each year of this study give a significantly positive correlation ($r = +0.49$, 17 d. f., $P < 0.05$) suggesting that, in years when higher mortality causes more change of mates, increased divorce reinforces this effect.

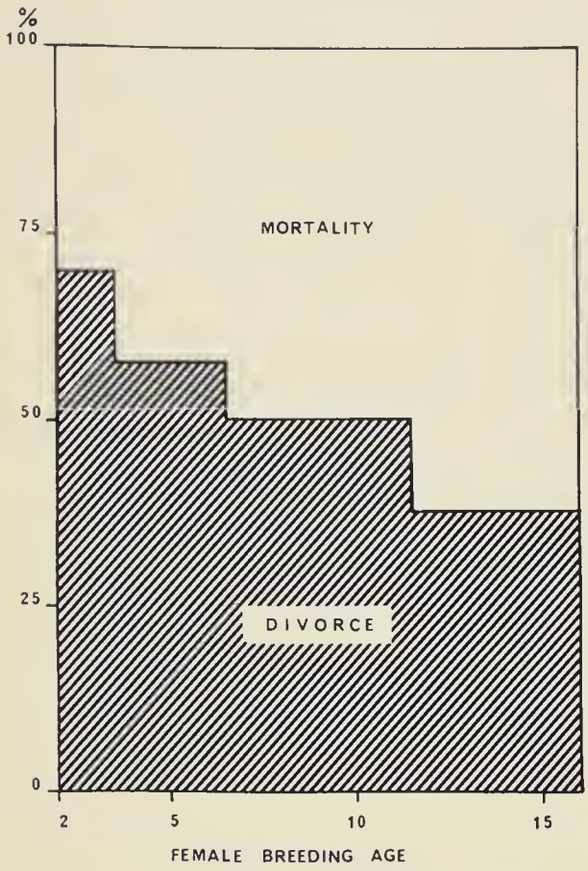

FIGURE 6. The cause of mate change amongst female Kittiwakes in relation to their age. Although the proportion of females changing mate varies little with age, the cause changes appreciably.

Effects of the pair-bond on the breeding biology

The effects on the nest-site tenacity. Very few pairs which retain the same pair-bond change their nesting site. On average only about 10 % of these pairs move to a new nest-site and this often involves a movement of less than 0.5 m. In contrast, males who change their mates are three times as likely to change their nest-site and the majority of females which change mate also change their nest-site (Fig. 7). A smaller proportion of the birds whose mates have died than birds which have divorced move nest-site, and this difference is particularly large and significant in the female ($P < 0.01$). Presumably this stems from the fact that both members of a divorced pair are still alive, present in the colony and wish to retain their previous nest-site, whereas when one of the pair has died, the competition for that nest-site comes only from other birds which have not previously owned that site. The difference in the proportion of divorced and widowed females changing site reflects the dominance of the male in retaining a site when it is in competition with the female who was formerly his mate. Fig. 7 also shows the marked age effect in the female with respect to retaining the nest

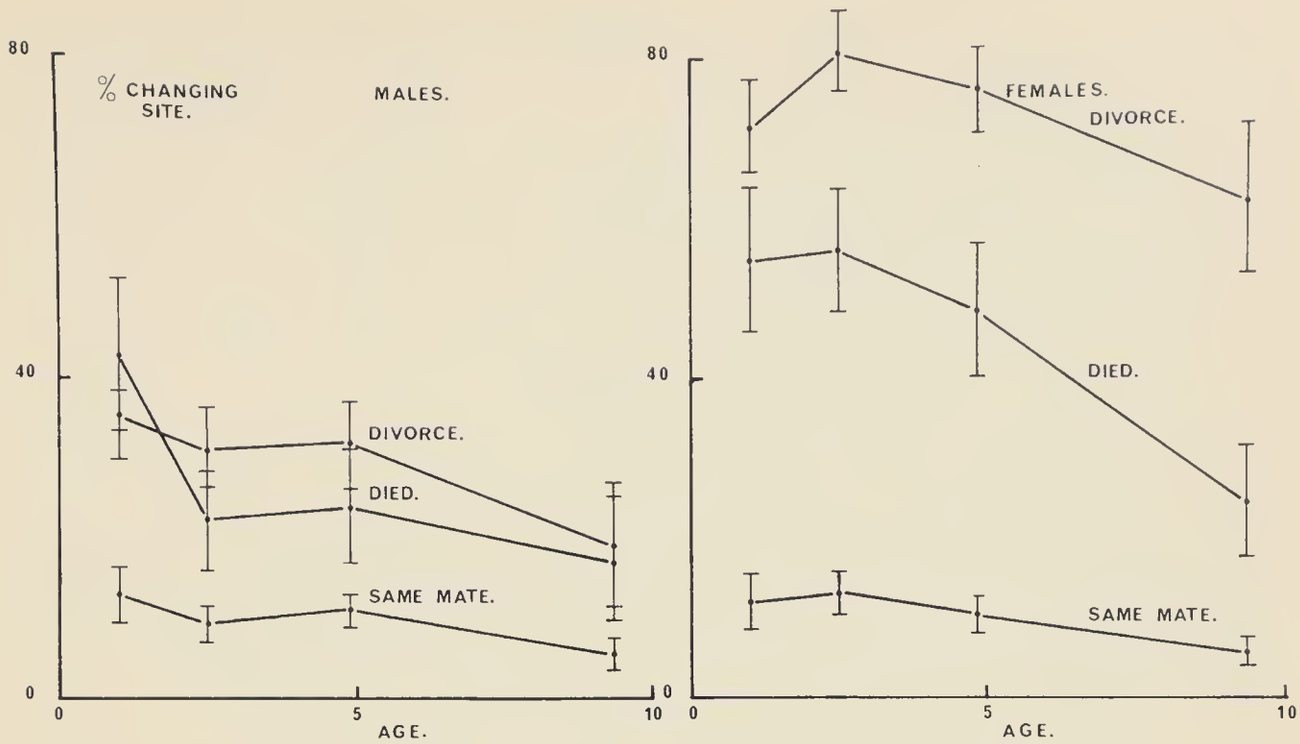

FIGURE 7. The proportion of male and female Kittiwakes changing nest site in successive years according to whether they retain the same mate, divorce or their mate of the previous year had died. Note the general decline in the trend lines with increased age and the large differences in the female groups related to the change in pair status.

site. The majority of old females retain their nest-site when changing mate and it has already been noted that these females also take young males as their new mates. This development of dominance in the old females is in contrast to the behaviour of young birds where the male is dominant and both selects and retains the nest-site.

The effect on breeding date. Birds which change their mate tend to breed slightly later than those birds of comparable age which have retained their mate from the previous year. Table 5 shows the delay in breeding is greater in the older birds ($P < 0.02$) and thus the change of mate has a greater influence on laying date in the older individuals.

The effect on clutch size. Change of mate has an effect on clutch size but it is more pronounced at the centre of the colony than at the edge. The data presented in Table 6 show that at the edge of the colony the clutch size is little if at all affected by change of mate. In contrast, at the centre of the colony, the birds which change their mate lay significantly smaller clutches. Since the mean clutch size of birds with a new mate at the centre and at the edge of the colony is the same (2.06 eggs), it would

TABLE 5. The effect of changing mate on the date of laying in relation to the age of the female (effect of centre or edge nest site removed)

	female breeding for		
	2—4	5—6	more than 6
sample size	524	228	381
mean delay caused by changing date (days)	0.72	1.23	3.56
S.E.	0.73	1.15	0.92

TABLE 6. The influence of nest position and change of mate on the clutch size of the Kittiwake

clutch size	edge		centre	
	change	same mate	change	same mate
c/1	13	17	16	10
c/2	184	170	197	230
c/3	26	40	31	116
total	223	227	244	356
mean	2.06	2.10	2.06	2.30
X^2	4.02		33.3	
P	n.s.		< 0.001	

The difference between the clutch size of females which retain their mate at the edge and centre of the colony is significant ($X^2 = 20.3$, $P < 0.001$). Birds taking a new mate showed identical clutch size at the centre and edge.

NOTE: The mean clutch size of birds with a new mate did not change with an increase in age.

appear that the retention of the mate in the centre of the colony has a greater stimulatory effect. There is no change in this effect with age.

Number of young fledged. The number of young fledged is influenced by (i) age, (ii) centre or edge effect, (iii) retention of a previous mate. These effects are illustrated in Table 7. Older birds fledge more offspring and young, edge birds do not breed as well as young, centre birds but this effect is less pronounced or even absent in older birds. Further, older birds which retain previous mate are more successful than any other group. It would appear that whilst the position of the nest is of paramount importance to the breeding success of young birds, the retention of the mate causes the main effect in older birds.

TABLE 7. The influence of age, nest site position and change of mate on the numbers of young fledged (sample size in parentheses)

site	pair status	age of female	
		2—4	over 4
edge	change	1.30 (133)	1.34 (90)
edge	same	1.25 (97)	1.66 (130)
centre	change	1.37 (133)	1.32 (111)
centre	same	1.46 (136)	1.59 (220)

How is the pair-bond maintained and how does divorce occur?

Divorce rate is higher in young birds than in old ones, it is higher in years with above average adult mortality and is inversely related to the duration of the pair-bond. It is clearly an important component in the biology of the Kittiwake but it is all too easy to draw human analogies. For many reasons, it is evident that the mechanism whereby divorce occurs in the Kittiwake must be a relatively simple process operating in a mechanical rather than a thoughtful and conscious manner.

It is our belief that most divorce in the Kittiwake stems from the two members of the pair returning to the colony at very different dates. The pair-bond is maintained by the two birds synchronising their return to the colony. Obviously time as such is only a crude measure of the opportunity of the birds to form a new pair-bond before their previous mate returns. Nevertheless we have examined the date of return to the colony of birds which formed a pair in the previous breeding season. Those which reformed the same pair were seen at the colony with a mean difference between the two birds of 10.8 ± 0.98 days (sample size = 198). In contrast the time-lag for pairs which divorced was 22.2 ± 2.87 days (sample size 52) and this difference is highly significant ($P < 0.01$).

Older birds have a lower divorce rate; they also show less variation in the date of return of the members of the pair. Thus a sample of 119 pairs of young birds (breeding for less than the fifth time) and which retained their mate, had a mean difference in the date of return of the pair members of 13.3 ± 1.4 days whereas a sample of 79 pairs of birds which had bred on more than 4 previous occasions had a mean difference of only 7.7 ± 1.2 days. Again the difference is significant ($P < 0.01$). These results suggest that it may be possible to explain much about divorce in the Kittiwake simply in terms of the date at which the two members of the pair return in the following spring. Further investigations are in progress and it is hoped that these will lead to a better understanding of how the pair-bond is maintained and how divorce occurs.

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SYMPOSIUM ON IMPRINTING

7. VI. 1978

CONVENERS: K. IMMELMANN AND S. SJÖLANDER

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Hormones and Filial Imprinting

Johann-Wolfgang Landsberg

The concept of sensitive phases

In his famous companion-paper Lorenz (1935) described imprinting as inductive determination in analogy to induction in embryological development. This viewpoint is supported by the fact that the sensitive phase is limited to a definite period in which imprinting may occur and by the fact that the imprinted stimulus remains very stable. Primacy, unrewarded learning, and irreversibility are also typical characteristics of imprinting. These characteristics suggest imprinting is an unique process different from other types of learning. Recent research on neuromuscular development, hormonal state, and probability of pharmacological influence may give a physiological basis to the psychological problem of imprinting and help verify the model.

The multi-dimensional model

The above mentioned characteristics were contested by the ongoing studies of imprinting phenomena. There is now evidence on the importance of sound, temperature, and light during embryological development and for posthatch conditions, the importance of rearing, training, and testing on imprintability. Especially, conditions of rearing have significant influence on the beginning and duration of the sensitive phase, and on the strength and stability of imprinting (Bateson, 1966). Familiarity and unfamiliarity of stimuli, e.g. colour or shape, affects the subsequent result of imprinting. This has been called perceptual learning by Bateson (1964). Summarizing many experimental results and theoretical reflections Hinde (1970) explained the imprinting phenomenon by saying it "should perhaps be regarded as an artificially isolated part of a process of learning about the environment" (p. 518). Detailed analyses show that there are several sensitive phases, superimposed on one another, which are related to different aspects of imprinting (Fabricius, 1964). Recent analyses also show different time-dependent responses to imprinting stimuli (Csány et al. 1973), and the divergent development of preferences for familiar and novel conspicuous objects after different periods of exposure (Bateson & Jaeckel, 1976). Obviously, imprinting seems to be a development of behaviour that includes a complex of different processes. "The sensitive period is not sharply defined—there is a rather gradual change in the ease or probability of learning, and its limits depend on the circumstances of rearing and the methods of testing" (Hinde, 1962, p. 247). "Each stage of development depends on an interaction between organism and environment at a previous stage, and the clock cannot easily be put back" (loc. cit., p. 249).

The uni-dimensional model

Recently attempts have been made to explain imprinting using general factors, such as intellectual faculties, attitudes, and motivation. Bischof (verb. comm.) describes a

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model, simulating the increase and decrease of probability of being imprinted. This is a time-dependent process of increasing restrictions upon imprinting stimuli. BISCHOF developed a function of distance to the imprinting object during training and its effects during testing. BATESON (1973) analysed the increasing preference for familiar companions and objects. Subjects also showed a preference for those objects slightly different from familiar ones. These findings were simulated by the effect of the simple function of familiarity and novelty of an object being applied to the imprinting process. Similar to the models discussed above, BATESON (1978) developed one to interpret the factors influencing sexual imprinting. These factors interact and may compensate one another. BATESON's model is simple and includes only one endogenous variable which represents the sigmoidal increase of intrinsic motivation to respond to an imprinting stimulus.

The relevance of hormones

The second and third theory are not mutually exclusive. They may simply represent different stages of scientific analysis. The first model describes the phenomena on the surface, while the second one characterizes general traits of behaviour and its development. In order to prove the models it is necessary to look for common factors in factor analysis. A correlation with hormones may help to explain factors of such a kind. The coupling of endocrinological and environmental factors could explain the high stability of this special type of learning (BUCHHOLTZ, 1973).

Testosterone

General interest in sexual imprinting is responsible for the research on chickens and ducklings, which are injected with sexual hormones, the outcome of which gives some relevance to research on the topic of filial imprinting. The application of testosterone increases the search for a particular type of food (ARCHER, 1974), the facilitation of copulation, and attack in male chicks (ANDREW, 1972 a). ANDREW (1972 b) used the hypothetical construct "persistence" in interpreting these phenomena, while CUMMINS et al. (1974) preferred the arousal-hypothesis, which assumes increasing arousal promotes imprinting. They found "cheeping" in chickens after injection of small doses, but no cheeping was apparent after injection of higher doses. These alternative explanations, arousal or persistence, are relevant with regard to research in filial imprinting, but there is no answer at present to this question. There is also a further handicap. Neither metabolism nor the normal concentration of testosterone in young male chickens is known. So, we do not know if an injection is physiologically effective or not. This is, however, of general significance in current research (ANDREW & ARCHER, 1977 and CUMMINS et al., 1977). The interpretation is very problematic if the dosage of injected hormones is higher than the natural concentration. See also SCHLEIDT (1964) where he suggests in the method of substitution to alter the concentration but only within the confines of the natural variance in the population.

Thyroxine

Many factors may lengthen or shorten the sensitive phase. HESS (1959 a) believes that the maturing motor ability is responsible for an increase in imprinting behaviour.

Obviously, high general activity will force imprinting, therefore, it is probable that a high concentration of thyroxine will enhance the effect of imprinting procedure. But there are no publications concerning this topic although it is known that thyroxine does accelerate development of behaviour in mice (Murphy & Nagy, 1976). Results like these are to be expected in chickens and ducklings, since Hess (1959 b) proved the law of effort to be effective in these species. According to his theory the degree of imprintability is dependent on the amount of effort exerted by the ducklings in following the object to be imprinted.

Adrenaline

Since the publications of Spalding (1875) and Lorenz (1935) other authors have indicated a correlation between the end of the sensitive phase of the following response and the onset of fear (Fabricius, 1951, Hinde, 1955, & Hess, 1959 a). However, interpretations are as controversial as the observations are unequivocal. The absence of an imprinting stimulus may stimulate fear behaviour (Kaufman & Hinde, 1961, Salzen, 1963), so "explanations in terms of purely endogeneous changes in motivation must be rejected", stated Bateson (1964, p. 100), thus favouring multidimensional models of imprinting. On the other hand exclusive interpretations in terms of social experience were also rejected because of Hess's findings of an onset of fear in inexperienced chickens, and that familiarity alone is not sufficient for the emergence of fear (Hoffman & Ratner, 1973).

Activation of the adrenal glands has been proposed as an origin for the onset of fear (Salzen, 1962, 1963), which prevents imprinting. The subcutaneous injection of adrenaline facilitates onset and duration of immobility reactions (Braud & Ginsburg, 1973). This method of experimentation is as problematic as experimental application of testosterone. Moreover, the natural concentration of adrenaline in young nidifugious birds is also unknown. Another method was used by Sparber & Shideman (1968); they administered reserpine to developing embryos and newly hatched chickens to reduce the influence of adrenaline. Reserpine given to 15 day old embryos caused a significant increase in following behaviour 11 to 38 hrs after hatching. Chicks one week of age, hatched from eggs injected with the drug prior to incubation, exhibited fewer avoidance responses in a conditioned situation. Summarizing, the birds show more following response and less avoidance behaviour when the influence of adrenaline is reduced with reserpine. Under these conditions the reduced influence of adrenaline may be augmented by injections (Schleidt, 1964) to demonstrate the effect it has on imprinting.

Corticosterone

Whereas adrenaline is responsible for short-term effects after stress, corticosterone—the other hormone from the adrenal glands—is responsible for long-term effects. Its secretions are elicited by the hypothalamus, which controls the secretion of ACTH. The corticosterone level increases during the sensitive phase. Many factors influence the concentration of corticosterone, e.g. time of day and posthatch age. The variability within groups of same posthatch age is large, and only 8 % (coefficient of determination) of this variance is due to increase in posthatch age, and the end of the sensitive phase (Weiss et al., 1977).

Favouring the arousal-concept, MARTIN (1973) imprinted Pekin ducklings and gave a retention test eight days after training exposure. The amount of time was recorded in which the ducklings followed a familiar and nonfamiliar object. Also the latence period before following began was recorded. A preference index was computed from this information, showing there is a non-significant tendency for the ACTH-injected animals to follow the model longer during the training period. The choice test shows clearly that the animals which receive ACTH are more strongly imprinted. The hormone may have increased the 'non-specific arousal' level during the training experience, resulting in stronger following and attention to the model.

Similar to the above discussion about testosterone and filial imprinting, the influence of corticosterone on imprinting is also controversial. Starting from the sensitive phase concept LANDSBERG & WEISS (1976) showed that corticosterone limits the sensitive phase. Pekin ducklings within the sensitive phase cannot be imprinted if they are exposed to stress prior to imprinting. Their corticosterone level is higher than that of ducklings 25 to 30 hrs of age, whose sensitive phase has already ended. Ducklings were less liable to be imprinted if physiological doses of ACTH were administered to them. Applied doses of ACTH, which are too small to prevent imprinting still cause a comparable increase of the corticosterone level after the beginning of imprinting, as do larger doses of ACTH. The secretion of corticosterone does not last as long, and during imprinting the corticosterone level decreases below the value found in ducklings 21 to 25 hrs of age, whose sensitive phase is ending at this point. The increase of the corticosterone level explains the increase of fear behaviour. Since only 8 % of the corticosterone increase is determined by age a series of environmental factors certainly must be controlling the hormone concentration, which in turn, elevated the amount of fear in the ducklings.

Discussion

Since KOVACH (1970) showed the specific relevance of the different theories based on the postulates of the sensitive phase on the one hand, and the interactive epigenetic interpretation or optimal arousal postulate on the other hand for the field of research on imprinting behaviour, several seemingly contradictory or alternative statements have been made. Each has specific consequences. MARTIN (1976) favoured the developmental age concept whereas LANDSBERG & WEISS (1976) favoured the posthatch concept. Reasons are given for these views and both concepts are not really alternative to each other (LANDSBERG, 1976 a). The sensitive phase measured by MARTIN is three times longer than the one reported by LANDSBERG. LANDSBERG & WEISS injected physiological concentrations of ACTH, only 1 % of the amount used by MARTIN, who did not discriminate between releasing and directing stimuli as LORENZ & TINBERGEN (1938) did (LANDSBERG, 1976 b). Summarizing, one can see that different results are the consequences of divergent viewpoints, theoretical implications, and experimental design, which are not alternative to one another.

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Beyond Sexual Imprinting

David B. Miller

Introduction

Over 40 years have passed since Konrad Lorenz (1937) posited the concept of imprinting to account for the means by which species recognition (with particular reference to mate selection) occurs in birds that do not "instinctively" recognize conspecifics. During this time, investigators have attempted to elucidate the process underlying imprinting mostly in the context of filial attachment rather than mate selection.

Most of this research has rendered exciting information on such factors as the effects of early experience on later behavior, sensitive periods in behavioral development, and the issue of reversibility versus irreversibility of preferences. However, I am uncertain about the extent to which 40 years of research have brought us closer to solving the problem initially posited by Lorenz pertaining to the development of normal, intraspecific sexual preferences.

In this paper, I discuss a means by which the experimental study of imprinting can more clearly and directly clarify aspects of normal behavioral development and present an example of this approach pertaining to auditory sexual imprinting in female Zebra Finches *(Taeniopygia guttata)*.

Conceptual strategies in behavioral development

To place this problem in broader perspective, let us consider two different, but potentially interrelated, conceptual strategies in the study of behavioral development. One strategy involves experimentally elucidating the parameters influencing normal behavioral development. In addressing this strategy, it is essential to gather normative, observational-descriptive data (preferably via naturalistic observation) to provide a baseline against which to compare data obtained via experimental manipulation (Miller, 1977). Such normative data should encompass not only species-typical motor patterns but also the most modal aspects of the environment in which the particular species lives (including stimuli provided by conspecifics and other species). The problem posited by Lorenz on the development of normal intraspecific mate preferences typifies this conceptual strategy.

The other conceptual strategy involves assessing a kind of plasticity by experimentally examining the extent to which behavioral development can be modified beyond (or assessed outside) the range of species-typical variability. It is important to recognize that this form of plasticity is not the same as that which is essential for normal adaptation and survival, but rather that which is manifest only in the realm of experimental manipulation. Most studies of imprinting (both filial and sexual) fall within the framework of this strategy by assessing the extent to which animals come to redirect species-typical preferences toward species-atypical objects.

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An underlying assumption behind the rationale of investigating imprinting in this fashion has been that the process may be general across a wide range of stimuli, both species-typical and atypical. Such an assumption, however, is risky without corroborative data.

A fundamental question regarding the experimental study of imprinting pertains to the possible relationship between data that elucidate the conceptual strategy of plasticity and the LORENZian question of normal species recognition. Figure 1 depicts a model illustrating the two conceptional strategies and their potential interrelationship. The regions of the curve marked A, B, and C represent types of studies that illustrate these particular strategies and points in between. Some types of investigations (type A) elucidate only behavioral plasticity in that they involve stimuli and/or assess motor patterns beyond the range of species-typical variation. Other types of investigations (type C) directly address the strategy of normal behavioral development by working well within the range of species-typical variability. Studies in region B are transitional and potentially serve to bridge the gap between the two conceptual strategies.

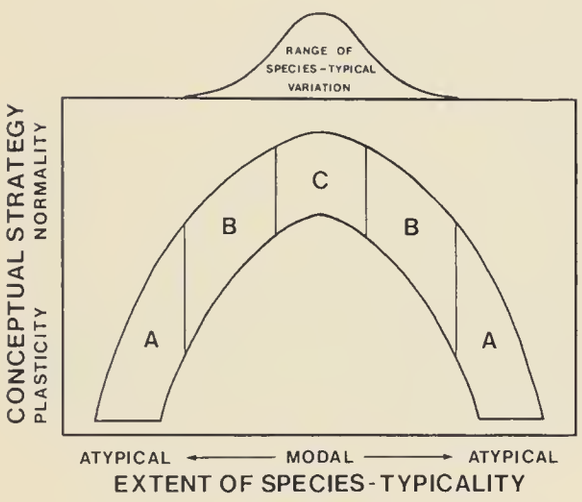

FIGURE 1. A model depicting the manner in which different types of investigations (A, B, and C) fall within the framework of, and elucidate the interrelationship between, the conceptual strategies of normal development and plasticity.

The ultimate issue of relating most laboratory studies of imprinting employing artificial stimuli to normal species identification (i.e., the generality of process issue discussed above) necessitates moving from investigation type A to type B, and eventually to type C. If the results are similar between types A and C, one can then conclude that the process is a general one.

What is needed, therefore, are more type C studies. With regard to sexual imprinting, for example, research programs involving interspecific cross-fostering (type A) can gradually pave the way for an assessment of intraspecific variables of a rather gross nature (type B; e.g., intraspecific cross-fostering of different color morphs that have a low incidence of interbreeding in nature), and gradually refine the analysis of preferences vis-à-vis the most modal aspects of species-typical stimuli (type C; e.g., subtle color shading differences within a color morph). Thus, by gradually refining the analysis to incorporate aspects that fall within the range of species-typical variability, studies that illustrate behavioral plasticity can, indeed, come to elucidate the course of normal behavioral development.

A reformulation of the original imprinting question, and an exemplifying model

One confounding aspect with regard to taking an intraspecific approach to the study of sexual imprinting is that most studies (of both filial and sexual imprinting) that assess the preferences of Kasper Hauser animals reveal instinctive preferences for conspecifics. However, it is important to recognize that these predispositions may be strengthened or sharpened via an imprinting process. Thus, one can further refine the initial question posited by LORENZ by asking how organisms that instinctively prefer to mate with conspecifics come to prefer certain individuals over others.

This brings us to a recently proposed model by BATESON (1978 a), according to which sexual imprinting serves as a means of regulating the extent of inbreeding and outbreeding among conspecifics. According to BATESON's model (depicted in Figure 2), an organism will show the strongest preference for a stimulus that is "optimally discrepant" from a familiar stimulus along a dimension of increasing novelty. Thus, the stimulus of optimal discrepancy must be somewhat similar, but neither too similar to nor too novel from, the imprinted stimulus, which, in the case of sexual imprinting, would usually be parents and/or siblings.

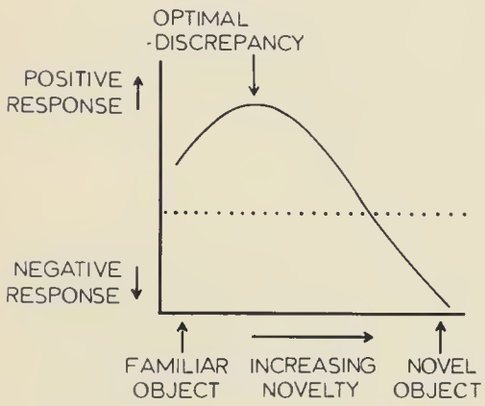

FIGURE 2. The postulated relationship between the sexual responses to an individual and its degree of novelty relative to familiar objects which would be kin under natural conditions. From BATESON (1978 a, 1978 b). Reprinted by permission.

To the extent that most species pair and mate exclusively with conspecifics in nature, BATESON's model can best be tested intraspecifically within the most modal range of species-typical variability (i.e., type C investigation). BATESON (1978 b) has recently corroborated his model by demonstrating that male Japanese quail mate with slightly novel females in preference to females to which they were exposed in early life, and both types of female are preferred to those with a grossly unfamiliar type of plumage. Working within a similar framework and attempting to extend the pioneering work by IMMELMANN (1972), I have been assessing the preferences of female Zebra Finches for conspecific auditory stimuli.

The acoustic basis of sexual imprinting in female Zebra Finches

In Zebra Finches, the ultimate choice of mate is made by the female who is typically courted by several males. Thus, an assessment of the parameters influencing the female's choice of mate is of obvious biological relevance. A recent study by SONNEMANN & SJÖLANDER (1977) reveals that female Zebra Finches are indeed imprintable despite an earlier report to the contrary (WALTER, 1973).

In nature, young male and female Zebra Finches typically leave the parents between days 30 and 40 and form mixed flocks with other young conspecifics, also coming in contact with other species. Sexual maturity is reached by 90 days of age (SOSSINKA, 1974). Thus, in early development (i.e., before day 40) females are exposed to the song of their father, and thereafter to the developing songs of male siblings that typically bear some resemblance to the father's song (IMMELMANN, 1969). Moreover, male Zebra Finch song is extremely variable interindividually and relatively stable intraindividually, thus providing a possible acoustic basis for individual recognition (MILLER, 1979).

The strategy of the following studies was to assess the extent to which the father's song type may influence mate selection by sexually mature female offspring.

Procedure

Around 35 days after hatching, female fledglings were separated from their parents and housed in a soundproof room with other young female Zebra Finches. Around day 100, each female was given a single 30-min simultaneous auditory choice test involving the song of her father and the song of another adult male Zebra Finch.

The rectangular test apparatus, housed in an anechoic chamber, was divided into two approach zones at opposite ends separated by a neutral zone, each zone being 70.5 cm long. Two loudspeakers were located outside the apparatus adjacent to each approach zone (see MILLER, 1979, for further details).

Two different groups were tested. In the first group, the auditory choice tests involved the father's song versus a stranger's song that was rather dissimilar in acoustic structure from the father's. In the second group, the stranger's song was somewhat similar to the father's song, as determined via comparisons of sound spectrograms. A preference was defined as having spent twice as much time in one approach zone than in the other for a minimum of three minutes.

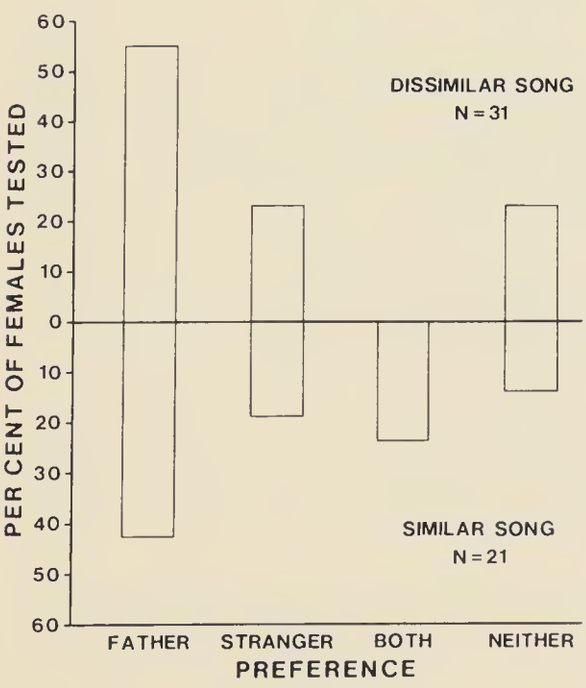

FIGURE 3. Per cent of female Zebra Finches that preferred their father's song, preferred the stranger's song, had no preference in that they found both songs equally attractive, and did not respond to either song in 30-min simultaneous auditory choice tests. Data for females tested to father versus stranger with dissimilar song are plotted above the line, and data for females tested to father versus stranger with similar song are presented below the line.

Results and discussion

The results are presented in Figure 3. When the stranger's song was dissimilar from the father's, the females preferred the father's song ($p < .05$). When the stranger's song was similar to the father's, the preference for the father's song was attenuated ($p > .05$), and a greater proportion of the birds preferred both songs equally; however, there was still a trend for the females to prefer the father's song, and the attenuation could be explained in terms of difficulty in discriminating between two similar songs.

Since the females did not prefer the stranger's song that was similar to the father's song but rather tended to prefer the latter, these data do not support BATESON's model. However, since the dependent variable was approach rather than sexual behavior, the preferences exhibited by these females may not have been sexually motivated (see also SONNEMANN & SJÖLANDER, 1977). At the very least, these data (still of a preliminary nature) demonstrate a remarkable long-term memory for a familiar stimulus as a function of early exposure.

Experiments of this type provide an example of the sort of intraspecific investigation that can be carried out in the framework of assessing the parameters that functionally contribute to normal, species-typical mate selection. If, in the next 40 years, we hope to come closer to elucidating the original concept of imprinting as posited by LORENZ than we have in the past 40 years, we must extend our experimental paradigms beyond sexual imprinting as it has been studied interspecifically and attempt to identify the intraspecific parameters underlying the development of sexual preferences.

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A Methodological Critique of Imprinting

Sverre Sjölander

Introduction

Among the reasons why imprinting has attracted so much interest is that it can be conveniently studied in the laboratory in rapid, easily replicated experiments, so that a long, cumbersome period of naturalistic observation is (seemingly) not needed, and that the phenomenon of sensitive phases (critical periods) for the learning is a novelty in learning theory. Two main areas of research have been lumped under the term imprinting, filial attachment and establishment of sexual preferences, which is understandable since both involve a preprogrammed learning, a sensitive phase for this learning and finally a great resistance to later change which may amount to irreversibility (Immelmann 1972).

Some methodological problems

The concentration of imprinting research on a few easily studied processes in even fewer species obviously involves risks for methodological difficulties as well as risks of overestimating the generality of the findings. The following reaction of young Mallard ducks *(Anas platyrhynchos)* is a good example. Here, the reaction can be elicited by almost any object that moves and gives rhythmically repeated sounds (Lorenz 1935, Fabricius 1951, 1962). The reaction shows an elicitation peak a few hours after hatching (Hess 1962). However, naturalistic observation of Mallards has shown that the young normally spend this sensitive period on the nest under the mother, only occasionally moving around her and not following her around (Bjärvall 1967, Hess & Petrovich 1973, Miller & Gottlieb in press). This may be resolved if one thinks of the following reaction as an emergency system, which in nature only is activated for short periods, e.g. when the mother leads the young to water or away from a dangerous situation. This particular system could use rather coarse clues to recognize the mother, since there is little chance of making mistakes. That does not mean that the young could not, at the same time, use far more refined clues to recognize the mother under undisturbed circumstances, and it is thus questionable to generalize from the simplicity of the eliciting of the following reaction to species recognition in itself.

This leads to another difficulty, which is to choose relevant overt behaviour through which one can measure the effect of early experiences. Instead of discussing these parameters, necessarily different for different species and leading to fairly sterile quibbles over what cases should be regarded as imprinting, it seems to me that an "internal" model gives a better handle on the problem. Here, imprinting would be a phase-specific, lasting establishment of a connection between an outer stimulus complex and a motivational system. In e.g. species recognition, a bird has to learn to recognize not only its own species but other species as well. The recognition of these other species, however, does not get connected to the sexual motivation. Likewise, in filial imprinting

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other things in the environment than the mother get to be known and recognized, but only she becomes an object of attachment. A similar reasoning may apply to acquisition of e.g. habitat and food preferences (e.g. Burghardt 1973).

Since motivational states vary, and the degree of connection between the stimulus complex and the motivation might be individually different, a preferable method in imprinting research is to measure preferences in simultaneous choices, rather than measuring e.g. following intensity, courting activity or distances between subject and object. Such a choice is obviously difficult to arrange, since the objects may not only vary in e.g. colour, but also in vitality, courting intensity, degree of synchronization with the subject, etc. Dominance relationships may also be important, as illustrated in an experiment on mating preferences in two colour morphs of a cichlid fish *Cichlasoma nigrofasciatum* by Weber & Weber (1976). They did not find any preferences due to early experience, but the experiment was conducted in such small aquaria (30 l) that only one fish of each sex was dominant, and thus dominance was the important choice factor, not the colour. Using the same species and the same colour morphs, but in a free-choice experiment where 144 individuals of different colour and experience were allowed to pair off in a large tank (4000 l), Fernö & Sjölander (1976) found a significant preferential mating according to experience. In a similar free-choice experiment also involving two colour morphs, of the Zebra Finch *Taeniopygia guttata*, Immelmann et al. (1977) found an almost total preferential mating according to early experience, wheras in laboratory choice situations the preferences shown are rarely as clear-cut (Immelmann 1969, Sonnemann & Sjölander 1977). Such free-choice situations are obviously difficult to arrange, but are so desirable that the possibility of realizing at least semi-natural ones (Schutz 1965, 1975) should be taken into account when planning investigations.

The different roles played in pair formation by male and female is a further difficulty in arranging experiments. A male should make a quick decision and then concentrate his courtship on a particular female, in order to compete better with other males. A female can afford to take more time to make a choice, and has less reason to concentrate her attention on one male, at least in the beginning of the choice process. Whereas a two-way choice may thus accentuate a male's preferences, a choice situation for a female should be arranged as a long-term choice between several objects (Klint 1976, Sonnemann & Sjölander 1977).

Sex differences may also occur already in the imprinting situation, creating further difficulties. Experiments in progress clearly indicate that males of the Zebra Finch get imprinted on their mothers, whereas the females get imprinted on the fathers (Immelmann & Sjölander in prep.). This gets further complicated by the dominance relationships among siblings, which may influence later sexual preferences (Kruijt pers. comm.).

The difficulties created by using abnormal stimuli for imprinting have been pointed out elsewhere (Miller 1980). In searching for a more biologically relevant method, single-clue imprinting seems promising, i.e. experiments where only one clue in the object of imprinting (otherwise quite normal) is changed. Experiments in progress show that by e.g. changing the bill colour of Zebra Finch parents, the young will later show sexual preferences for partners with such bill colouration (Sjölander in prep.).

The assumption here is of course that conspicuous markings are the ones most likely to be imprinted, and that the pre-programming or predisposition tells the bird where or what to "look for", but not the exact characteristics of the clue. One way to detect such relevant clues could be to look for characteristics that show comparatively much individual variation. If an important function of sexual imprinting is to facilitate population separation, as repeatedly suggested (e.g. Immelmann 1975, Bateson 1978) the system would obviously profit from easily detectable individual differences in imprinting objects and prospective partners. A mutual adaptation of the two systems should take place, so that the imprinting mechanism should exert a selection pressure on variable clues, and the variable clues would counteract on the imprintability and the ease with which such clues are detected and learned. Dialectical bird song might be a good example of such a coevolution.

Conclusion

From a methodological point of view, imprinting is an area of behavioural research where there are many risks of running up blind alleys, due to the considerations mentioned above. An obvious suggestion is that future research could profit from a more naturalistic approach, concentrating on three aspects, the What, When and Why of imprinting.

By What I mean the investigation of the stimuli imprinted and the imprinting predisposition, as a system where the two sides are adapted and geared to another. This would thus involve not only the hitherto common concentration on the imprinting mechanism itself, but also an analysis of the stimuli to which this mechanism is geared.

In investigating the When, i.e. the sensitive phases, it seems obvious that this should relate to the life history of the species, since an animal should of course be most imprintable at the stages in its ontogeny when it first meets, or has to cope with, the relevant stimuli. The length of the phase should be expected to be adapted to the time it would take to get acquainted with all relevant aspects of these stimuli, and the phase should come to an end whenever the animal starts to run the risk of getting imprinted on wrong objects (e.g. when leaving the parents). Investigation of sensitive phases seems to be especially interesting in studying socialization processes (e.g. Ågren & Meyerson 1978).

In asking the Why question, the life history of the species is again a keystone, since the reason why a species has acquired a capacity for individualized recognition of something, whether it is its own species, food or habitat, obviously lies in ecological factors that have exerted selection pressures in this direction (Immelmann 1975). One still debated but very plausible reason for individualized species recognition lies in the population separation mechanism mentioned above; other reasons might lie in competition reduction or sociobiological aspects.

Imprinting thus is a term that covers many different aspects of early experience, and it is difficult to find a border-line to other types of learning, since there seems little reason to think that the stimulus perception, memory storage or connection between motivational systems and releasers is different in imprinting. Even the most typical feature, the phase specificity, seems to exist to different degrees in other learning as well. It may thus be that imprinting simply constitutes those cases where phase-specificity and mem-

ory persistance are most obvious to the human observer. The term will obviously retain its didactic value, but it should not lead one into believing that it denotes a unitary phenomenon, and thus into conceptual and methodological difficulties.

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Field Experiments on Problems of Imprinting to the Birthplace in the Pied Flycatcher *Ficedula hypoleuca*

Rudolf Berndt and Wolfgang Winkel

Introduction

It is a well known phenomenon from numerous recoveries of ringed birds that migrants generally return to breed in the approximate vicinity of their birthplace. The term "Geburtsortstreue" (fidelity to birthplace) is applied to this phenomenon (cp. e.g. Drost 1953, Schüz 1971). Up to now, however, little is known about the controlling factor(s). We have started field experiments with the Pied Flycatcher, *Ficedula hypoleuca,* directed to this complex of questions. This report deals with the following question: Is returning ability genetically based, imprinted (learned) or a combination of both components?

Materials and methods

Our studies on the question of imprinting on the birthplace were made from 1975 to 1977 in our research areas near Wolfsburg (especially in the Drömling, East Lower Saxony; 52.31 N, 10.54 E) and Lingen (Elbergen Forest, West Lower Saxony; 52.27 N, 7.15 E) which lie about 250 km apart. More details about these areas are given in Berndt 1960, Berndt & Winkel 1967 and Winkel 1975.

The experiments in 1975 consisted of a reciprocal exchange between the two study areas of both eggs (at different stages of incubation) and nestlings (7—14 days old). In 1976, nestlings were handreared at the birthplace in the Lingen area, caged there until past the date of fledging, and later released in the Wolfsburg area.

For proof of possible settlement in one area or the other, we undertook, during 1976 and 1977, a control capture in both study areas of all males and females of *Ficedula hypoleuca* found in the nest-holes.

The experiments and their results

Transportation of eggs and nestlings

To clarify the question of which area Pied Flycatchers return to for reproduction when transported to a different locality as embryos, we exchanged clutches, in 1975, from the Wolfsburg area with others from the Lingen area and vice versa. In Experiment 1, 107 nestlings fledged from eggs transferred from Wolfsburg to Lingen and in Experiment 2, 47 nestlings fledged from eggs transferred from Lingen to Wolfsburg. In the following years, five individuals from the first experiment were found as breeding birds near Lingen and four from the second near Wolfsburg. All nine recaptured Pied Flycatchers had thus returned to the place from which they fledged after transport there in the egg, None could be shown to have returned to their actual place of origin.

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As nestlings, 29 birds were transported from Wolfsburg to Lingen and 38 from Lingen to Wolfsburg. Of these young birds which fledged in areas that were not their birthplace (Experiments 3 and 4), two and five individuals respectively were found again in their fledging areas and none in their place of origin. Our findings correspond with the result of Poliwanow and Schtscherbakow (according to the consolidated report of Mauersberger 1957) for East European Pied Flycatchers, which were transported over distances of 400 km and 50 km. Similar findings also exist for the Collared Flycatcher *Ficedula albicollis* (Löhrl 1959), the Short-tailed Shearwater *Puffinus tenuirostris* (Serventy 1967), and the Herring Gull *Larus argentatus* (Drost 1958) (also see Schüz 1938).

The evidence that knowledge of the birthplace is not inherited should be no surprise since it is hardly conceivable that each individual has instinctive (innately fixed) knowledge of its own birthplace.

Transportation of young birds after rearing and caging at the birthplace

Building on the results of Experiments 1—4, we tested in a fifth experimental series the reaction of young Pied Flycatchers which were kept in cages at their birthplace for nearly three weeks beyond the potential fledging date (age of approximately 36 days), and only then transported and released. For these experiments, we used 80 young birds from the Lingen area which had been handreared there, kept caged until 4 July and then released near Wolfsburg on 5 July. In the following year there was evidence of five return recoveries,—all from the release area near Wolfsburg. This finding indicates that the birds kept caged at their birthplace for almost three weeks a) were not influenced there in relation to the definite establishment of the "home place", b) that a definite fixation is possible even about three weeks after the potential fledging date, in other words at or after the actual fledging (= time of release) and c) that the short period of time available up to the beginning of the autumn migration was still sufficient to effect a definitive "home attachment".

On this point, to our knowledge, only Löhrl (1959) carried out comparable investigations, on the Collared Flycatcher *(Ficedula albicollis)* and he obtained similar results to ours with the Pied Flycatcher.

Discussion of the results

As the possibility of genetic attachment to the birthplace could be excluded, it remains to ask: is fixation on the home area, to which it attempts to return on the homeward migrations in later life, produced in the Pied Flycatcher by an imprinting in the strict sense, or an imprinting-like phenomenon, or another type of learning process?

The last can be virtually excluded on the basis of the known migratory behaviour of this species. An individual that has departed to its winter quarters in autumn would theoretically find its way back to its home place in view of the fact that in spring it would merely retake in the reverse direction the route learned on the outward journey (cp. W. & R. Wiltschko 1976); however it is known that *Ficedula hypoleuca* returns home in spring by a route which diverges distinctly from that of the autumn migration

(Drost & Schilling 1940 and unpublished recovery material of the "Vogelwarte Helgoland"). The home place must therefore have been impressed upon the Pied Flycatcher in another way, that is to say fixation on the birthplace is a type of imprinting process (cp. Berndt & Winkel 1975).

Imprinting is involved, according to Immelmann (1969, 1970), when at an early age, during a sensitive period, a mode of behaviour is rapidly established and stabilized, through particular impressions from the environment (cp. e.g. Nicolai 1964). When one examines the returning behaviour of the Pied Flycatcher in the light of these imprinting criteria, the following points emerge:

1. Fixation on the birthplace takes place during an early ontogenetic phase and within a short time, since fledged young birds are as a rule in the habit of leaving very quickly—apparently even after a few days (cp. e.g. Drost & Schilling 1940; Curio 1959; Jones et al. 1977)—the exact hatching place to which they later return (cp. e.g. von Haartman 1949; Lichatschew 1955; Curio 1938; Campbell 1959; Berndt & Sternberg 1966). In experimental conditions, the fixation phase—possibly within the scope of a new imprinting—can also begin later (even, as we showed in our experiment 5, at an age of at least 36 days) and be successfully completed by the time of the early migration of this species (cp. Creutz 1955). According to Löhrl's (1959) findings, the imprinting phase in *Ficedula albicollis* can be narrowed down even further since, in his transportation experiments, fixation could partly have been brought into play no earlier than an age of about 45—50 days. Whether the lack of return recoveries in the Collared Flycatchers which were released by Löhrl at an age of about 60 days, and therefore after the end of their juvenile moult, is attributable to the end of the sensitive period, or whether the time left before migration was not sufficient for imprinting, or completely different causes exist, cannot be clarified. Normally, imprinting must in any case be concluded by the beginning of the autumn migration.

2. Fixation on the birthplace occurs in the Pied Flycatcher in a very lasting manner. Berndt & Sternberg (1966, 1969) found about 50 % of all the one-year old birds whose return was proved breeding at a distance of no more than 1000 metres from their respective birthplace. However, it appears that a considerably higher proportion first attempted to return to their birthplace but not all of them succeeded in taking over a breeding hole there. Consequently the losers in the intra- and inter-specific rivalry were compelled to space out in the adjoining areas (Berndt & Sternberg 1969, Berndt & Winkel 1974). The occurrence of such exogenously conditioned dismigration away from the birthplace is supported by numerous cases in our unpublished material on Pied Flycatchers who, in their first year, bred at a relatively greater distance from the birthplace, but resettled in later years in the area of birth (cp. Berndt & Sternberg 1965). In this way it is even probable that, of the Pied Flycatchers which breed at a distance from their birthplace in the first year, a relatively greater proportion, in general, return to the birthplace each year, and thereafter, if there is a renewed shortage of available breeding sites, only make for the foreign breeding place, occupied in the previous breeding period (cp. Berndt & Sternberg 1965, 1968). The great importance of spacing for the fulfilment of the dispersion pattern in the Pied Flycatcher is also an argument not in anyway against, but positively for an extensive imprinting to locality which, however, can frequently not be realized because of limiting factors.

3. Finally there remains the question as to what are the "particular impressions" from the environment imprinted on each individual in this fixation on the birthplace. At the present we have no data to deny or support any of the vast number of possible cues.

In summarizing our results and reflections, it seems to us that we are justified in interpreting fixation on the birthplace in the Pied Flycatcher, if not as classical imprinting in the strict sense (see Lorenz 1935), at least as an imprinting-like phenomenon (Immelmann 1976), although the possibility cannot be excluded that other learned components could also be involved in imprinting to a place.

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Communal Breeding in Birds: An Assessment of Kinship Theory

J. David Ligon

Introduction

Kinship theory (Hamilton, 1963, 1964) or kin selection has become a central theme of sociobiology. This concept is currently widely employed to explain apparently altruistic behaviour in animals ranging from insects to birds and mammals. Because different authors use the jargon associated with kin selection somewhat differently, it may be worthwhile to define or reemphasize some fundamental terminology.

Altruism. An altruistic act decreases the personal or individual fitness of the altruist (i.e., decreases its own reproductive potential). Hamilton proposed that altruism could be expected when the ratio of benefits (b) to the recipient, to costs (c) to the donor exceeds the reciprocal of the average coefficient of relationship (r): $b/c > 1/r$. Although this formulation is theoretically attractive, to date it has not been productive in field studies because meaningful measurements of costs and benefits of putative altruistic acts have not been achieved (Brown, in press).

It should be emphasized that the question of altruism is at the base of the controversy over the role of kin selection in avian communal systems.

Kin Selection. This term, introduced by Maynard Smith (1964), has been applied to Hamilton's (1963, 1964) theories on the evolution of altruism. Because Hamilton developed kin selection theory specifically to provide an explanation based on individual selection for apparent altruism, the term, at least historically, clearly connotes a loss in individual fitness.

Inclusive Fitness. The inclusive fitness (i.f.) of an individual organism is measured as its lifetime production of replicates of its own genetic material: i.f. = classical component (breeding or individual fitness) + kinship component (aid to relatives that decreases the classical component – i.e., is altruistic – but increases the fitness of relatives other than offspring) (Hamilton, 1964; West Eberhard, 1975).

Nepotism. Recently this term has been used interchangeably with kin selection to indicate altruism directed toward relatives (Alexander, 1974; Sherman, 1977). Because "nepotism" does not suggest altruism, I suggest that the term be restricted to those cases where relatives are aided with no recognizable cost to the aid-giver, e.g., cooperation (Hamilton, 1964) or mutualism between relatives.

A distinction of this sort between "kin selection" (altruism implied) and "nepotism" (altruism not implied) should damp the semantic differences between workers and help to focus on the important unresolved issues concerning avian communal systems. Note that unless altruism is demonstrated, the term kin selection, as originally defined and used, is not appropriate. In the following discussion "kin selection" is considered in this sense.

Kin selection has been used in conjunction with ecological variables to account for the apparent altruism seen in bird helper systems (e.g., Brown, 1970, 1974, 1975; Alvarez,

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1975; Ricklefs, 1975; Morton & Parry, 1974; Maynard Smith & Ridpath, 1972). In contrast a few authors have explicitly rejected kin selection as a major factor in the evolution of communal nesting (Zahavi, 1974, 1976; Woolfenden, 1976; Woolfenden & Fitzpatrick, 1978), instead emphasizing selfish strategies in a social environment. Various other studies have not dealt specifically with the theory (e.g., Rowley, 1965; Harrison, 1969; Dow, 1970; Ligon, 1970; Macroberts & Macroberts, 1976), or have employed "group selection" interpretations (e.g., Wynne-Edwards, 1962; Fry, 1972; Parry, 1973).

Here, I first attempt to draw attention to some general problems of kinship theory that have not been adequately addressed by ornithologists. Second, I illustrate some of these points by reference to studies in progress by my wife, Sandra, and myself on a communal African bird, the Green Woodhoopoe *Phoeniculus purpureus*.

General problems of kinship theory

Hamilton (1963) considered the spread of a single gene, the phenotypic expression of which conferred altruism toward relatives in proportion to the average relatedness between altruist and beneficiary. Subsequently, he (Hamilton, 1964) considers both the single gene hypothesis and r (the expected fraction of genes identical by descent in a relative). Most authors apparently accept the second view; i. e., the proportion of shared genes is the critical factor. This interpretation is followed here. However, the problem is far more complex than this assumption indicates.

Kinship theory ignores variance in genetic relationships, e.g., between sibs. Some writers treat parent-young and sib-sib relationships as exactly equivalent (e.g., Ricklefs, 1975; West Eberhard, 1975). However, a parent and its offspring *do* share 50 percent of their genes, whereas two full sibs share varying fractions of their genetic material (S.P. Hubbell, ms); thus, parent-young and sib-sib relationships cannot validly be treated as identical. Most communal birds produce few surviving young or have few surviving sibs; therefore, the genetic uncertainty involved in sib-sib relationships takes on great importance. That is, averages become less meaningful as sample size decreases.

Among communal birds, if a younger sib truly equalled an offspring in evolutionary units, why would an individual helper ever leave the security of its parents' territory and attempt to breed on its own? Ricklefs (1975) addresses this question, but his suggestions may be incomplete. An important point is certainty of relationship between parent and young, versus the uncertainty of average relatedness between two sibs. (Moreover, both parents can be more confident of their relationship to offspring – e.g., that the male has not been cuckolded or that extra eggs have not been placed in the nest – than offspring can be that they share both parents. In birds, where the number of close relatives is small, variance in genes shared may detract seriously from arguments based on average relationships.

Another problem concerning the use of average relationships pertains to what S.P. Hubbell (ms) refers to as a form of genetic drift; i.e., genes can be lost by chance. Such chance losses will alter the proportion of alleles shared between relatives in an unpredictable manner that further reduces the ability of an animal to determine the amount of genetic material it shares with another individual.

Theoretically, if kin selection is important, close inbreeding might be expected. (Inbreeding increases the number of alleles shared by two individuals.) BROWN (1974) reported inbreeding and an *r* value of 0.8 for Mexican Jays *Aphelocoma ultramarina*. Recently, he has withdrawn that estimate (BROWN, in press). No other workers has reported a high degree of inbreeding in communal birds. Rather, WOOLFENDEN (1976), WOOLFENDEN & FITZPATRICK (1978), and J.D. & S.H. LIGON (ms) find that replacements of a deceased breeder usually come from outside the flock and that parent-young or sib-sib matings do not occur in Florida Scrub Jays *Aphelocoma c. coerulescens* or Green Woodhoopoes.

Because kinship theory is basic to much of sociobiology, "altruism" in communal birds deserves close examination. Does the helping behaviour of birds, sometimes labelled altruistic (e.g., BROWN, 1970, 1974; RICKLEFS, 1975; WEST EBERHARD, 1975), in fact decrease the breeding potential of the helpers? At present, no evidence exists among communal birds showing such sacrifice. Rather, it appears that helpers generally do not have the option to breed for various ecological and societal reasons, and, moreover, have a greater chance of surviving to breed at a later time by remaining in the parental territory and engaging in activities favourable to their interests and to those of their parents – defending the territory, feeding nestlings, etc. (SELANDER, 1964). In some species extra birds apparently do increase the reproductive output of the breeding pair (EMLEN, 1978; BROWN, in press); however, it does not follow that the helpers are sacrificing anything in any meaningful way. Instead, helpers may gain directly by the production of younger birds (WOOLFENDEN & FITZPATRICK, 1978; see below). Moreover, active helpers and dependent young sometimes are unrelated (e.g., HARRISON, 1969; ZAHAVI, 1974, 1976; WOOLFENDEN, 1975; J.D. & S.H. LIGON, ms); in such cases a "kinship component" may be an inappropriate explanation.

In short, kinship theory involving altruism, although intuitively and theoretically attractive at one level, has several general weaknesses and has not to date been well supported by the most detailed studies of avian communal breeding systems. Thus at this time, it does not seem parsimonious to assume that kin selected altruism is the evolutionary driving force behind communal breeding. The remainder of this paper uses the social system of the Green Woodhoopoe to illustrate some of these general points.

Green Woodhoopoes and kinship theory

As in other communal species, non-breeding Green Woodhoopoes feed and defend nestlings and fledglings. Such aid need not be considered as altruistic in any sense, because helpers of both sexes clearly use younger flock mates of the same sex (often sibs) to gain entry and establishment in a new territory. Moreover, younger sibs later become provisioners for the oldest former helper's own young. Thus, young woodhoopoes in the nest represent an essential resource for current helpers. Nestlings can be viewed as an aspect of the helper's environment that, given the proper circumstances, can be utilized or exploited by helpers.

How do younger birds (beta) gain by leaving their parents' territory and moving to a new area with an older, dominant bird (alpha) of the same sex? Kin selection does not provide a convincing answer since offspring of the alpha bird are related to the beta bird at most by only an average of 0.25 (if alpha and beta are full sibs), whereas younger sibs of the

beta individual are related by an average of 0.50. Rather, a possible answer lies in the high and unpredictable mortality. The beta individual has as good a chance of attaining breeding status as does the alpha bird. In seven of nine cases where unisexual groups emigrated to a new territory, or where two males were found in small or new flocks, the alpha male died first, with the beta individual inheriting breeding status and other flock members as helpers.

The breeding pair also gains by the presence of helpers. First, helpers usually are their grown offspring. By staying at home the chances of the helper's surviving to breed almost surely are greatly increased. Second, more birds mean a larger territory with the additional resources contained therein. And third, to the extent that breeders with more helpers produce more young than do those in smaller flocks, the retention of grown young as helpers is adaptive for the parents.

Thus, within a woodhoopoe social unit, all categories – nestlings, helpers, and breeders – of both sexes can gain directly by the feeding of nestlings. At present I see no meaningful way to determine that one category gains more than the others, since each individual goes through all stages if it lives long enough.

Flock members unrelated to nestlings are sometimes helpers (in at least three of 22 studied flocks, or 14%), further weakening a kin selection interpretation. Being a member of a flock with an established territory, roost sites, etc., is surely of advantage to an individual woodhoopoe, whether or not it is related to other flock members. Moreover, even unrelated helpers may gain the use of nestlings in the helper's own future breeding program.

Breeding birds in adjacent flocks may be closely related (sibs or parents and young). Yet neighbouring flocks compete most intensely for space and the resources included therein. Because aggression between adjacent flocks is pronounced, it appears that individual selfishness is involved and that kinship ties between flocks are largely irrelevant to the birds.

In Green Woodhoopoes the "sacrifice" of a helper in feeding nestlings is analogous to the sacrifice of a typical temperate zone songbird that sacrifices time, energy, exposure to predation, etc., to gain a territory and mate. The goals are the same. The ecological and societal settings, however, demand different paths to the goals. Flock members, related or unrelated to nestlings, may use the younger birds to their own ends in exactly the same ways, and eventually the "used" young bird may gain in a like manner. Thus, in Green Woodhoopoes, genetic ties beyond those of parents and their offspring are not required to explain helping behaviour.

In 1971, E. O. Wilson (1971: 334) raised the question: Is kinship theory as developed by Hamilton both good and true, or is it simply good (in the sense that it has stimulated investigation into evolutionary mechanisms)? Kinship theory clearly has generated research into the mechanisms behind the evolution of complex social systems such as avian communality. However, to date altruism has not been demonstrated to be basic to this form of sociality in any bird species. However, at the least, increased success of genes shared between helpers and recipients can be considered as an evolutionary bonus to the helpers (G. E. Woolfenden and J. W. Fitzpatrick, pers. comm.). The extent of this "bonus" and its significance in the evolution of any communal system remain to be ascertained.

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The Origin and Role of Helpers in Bee-Eaters

M. Dyer and C. H. Fry

As Brown (1978) points out in the most recent and up-to-date review of communal breeding in birds, current studies are demonstrating that the species concerned are so diverse and fundamentally different from one another that they share hardly any traits other than helping behaviour. Even the helping behaviours and communal systems differ greatly (loc. cit., Tables 1, 2 and 4), although many of the low-hundreds of cooperative-breeding bird species fall into one of four or five rather clearly-diagnosed categories. The diversity of avian communal breeding systems makes them difficult to characterise, at least beyond the common possession of helpers; Brown contrasts communality with coloniality, and describes as typical attributes of the former: living in small groups, sedentariness and social stability, and group territorial defence. Of the family that we have been studying for many years, the bee-eaters (Meropidae), some communal-breeding species are, in contrast, highly migratory and all of them lack group territoriality. Many bee-eater species are of course highly colonial and the one that has been our principal concern, the Red-throated Bee-eater *Merops bulocki,* is in fact far more densely aggregated in its distinct breeding colonies than any of the few other colonial communal breeding birds (Brown, 1978, Table 4) except the unique Sociable Weaver *Philetairus socius.* Prima facie, the adaptive bases of communal breeding among bee-eaters will differ from those among other birds, and in our following consideration of the problem of helpers at the nests of bee-eaters our inductions may not apply elsewhere.

In at least two respects bee-eaters are particularly suitable for investigation of helping behaviour. The first respect is that, apart from two small and ill-known genera inhabiting Malesian rainforest, the family consists of species with such morphological uniformity that several recent authorities recognise only the one genus *Merops.* The absence of any but incipient radiation is doubtless attributable to the same dietary specialisation prevalent among *Merops* bee-eaters. It seems probable that specific variation in helping at the nest (some species without helpers; others with a large minority of nests having plural helpers) is a direct correlate of such other biological differences as are manifest between the species – geographical range, habitat, breeding season in relation to season of greatest adversity, migratoriness, coloniality, and the shape of the survival curve.

The second respect is that there is every gradation in breeding aggregation among bee-eaters, from essentially solitary species to those with colonies of tens, hundreds, or thousands of nests and, as Brown (1978) puts it, "colonial species are of interest because the home range of the colony is presumably freely available to non-breeders whether or not they associate with or help a particular pair. If this is true, the costs and benefits of helping can be separated from the fitness economics of territoriality, which seems important in non-colonial species". While our investigations of the costs and benefits of helping have far to go even with *M. bulocki,* we have initiated studies of four other species having differing colonial status (but not yet of *M. malimbicus,* which breeds in colonies of

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50 000 birds and will doubtless prove fascinating for students of communal breeding). Some life-history variables of these five African and European species are set out in Table 1.

Table 1: Some biological characteristics of five *Merops* spp.*

	M. bulocki	*M. pusillus*	*M. nubicus*	*M. albicollis*	*M. apiaster*
Range	Afr: n.w. tropics	Afr: sub-Saharan	Afr: n. tropics	Afr: n. tropics	s.w. Pal. (winters tropics)
Habitat	wooded savannas	grassy savannas	wooded savannas	steppe	all open country
Migratoriness (km)	sedentary	10s–100s	100s	100s–1000	1000s
Breeding season	dry	early rains	early rains	desert-edge 'rains'	summer
Breeding aggregation	colonial: 10s	solitary	colonial: 100s–1000s	loose	colonial: 10s–100s
Max. helpers/nest	3	0	(1)	5	1
%age of nests with helpers	30	0	<10	high	10?
Mean clutch	2.9	4.4	2.5	5.7	in range 4–9
Mean hatching interval (days)	1.0	0.6	1.7	?	?
Pullus growth rate constant K	0.324	0.296	0.260	?	?
Approx. fledglings/adult	1	>2	<1	2	$1^1/_2$
Approx. adult weight (g)	25	15	55	25	50
♂/♀ ratio	1.5	1.0	1.6	1.7	1.5

* Some comparable data for *M. bullockoides*, the southern tropical allospecies of *M. bulocki*, are given by Emlen (1978).

Merops bulocki

An outline of the biology of this species, which we have been studying at Zaria in northern Nigeria, was given by Fry (1972). About one third of the 20–60 nests comprising a colony have helpers, generally one each (occasionally up to three) helpers per nest. As in many other co-operative breeding species, aid-giving behaviour becomes more evident and important after the eggs hatch. Unfortunately we could be certain of the kinship of the helper in only a few instances. In all such cases the helper was the previous year's offspring of the pair of birds whose nest it was attending; in some other cases the helper may have been from the brood before that, two years earlier.

It has become evident, from our monitoring of the weights of individual nestlings and parents and helpers over the nestling period, how adverse is the season in which *M. bulocki*

breeds – from January to April, towards the end of a dry season of seven months unremitting drought. In normal periods at this time of year the flying insects (mainly Hymenoptera) on which *M. bulocki* feeds are still sufficiently abundant, although the weights of all classes of adult birds feeding nestlings then do decline somewhat. But in the period January (or December) to March, spells of harmattan weather are commonly encountered throughout the more northerly woodlands of the whole of West Africa, which are so severe that many nestlings starve to death. The harmattan is a dry, dust-laden wind blowing from the Sahara. Its intensity varies; in extreme cases the measured wind run may exceed 400 km/day, with visibility reduced to less than 0.25 km, the maximum mid-day temperature rising to only 22° C, and the relative humidity below 10%. Such a combination of wind, poor visibility, chill and drought depresses insect activity (Johnson, 1969) and consequently affects the feeding success of insectivorous birds. The varying ability of bee-eaters to cope during a harmattan is illustrated by observations during a six-day period of continuous harmattan. At two nests of birds breeding for the first time at one year of age, the broods were abandoned on the second day of the harmattan; but all broods in the adjacent nests of 20 older, experienced pairs continued to be provisioned, albeit at a low rate. Had the four birds of the two inexperienced pairs each spent an 'apprenticeship' season as helpers and then nested themselves the following year, they would have been less likely, it seems, to abandon their broods.

Table 2: *M. bulocki:* Brood reduction in broods of three and four provisioned by pairs and by trios (pair with one helper)

	total nests	nests suffering reduction	total dead young	% loss*		total nests	nests suffering reduction	total dead young	% loss*
	Broods of three					Broods of four			
Pairs	30	19	20	22	Pairs	3	3	3	25
Trios	7	1	1	15	Trios	4	2	2	13

* calculated as (number dead nestlings/total number young) × 100.

Bee-eater clutches hatch asynchronously and brood reduction (the selective starvation of younger nestlings when food is in short supply) commonly occurs. In *M. bulocki* the incidence of brood reduction is significantly lower at nests where helpers are in attendance than at nests without helpers (Table 2), and the significantly better survival to fledging of nestlings fed by three (rather than just two) adults is shown by the data in Table 3.

Table 3: *M. bulocki:* Number young fledged from broods raised by pairs and trios

	No. broods	Total young fledged	Mean no. young fledged/brood (± S.E.)
Unassisted pairs	56	112	2.0 ± 0.3 *
Trios	22	59	2.7 ± 0.3

* $t = 4.3$, $P < 0.01$

It is tempting to identify both the presence of helpers and the size differential within a brood as adaptations improving survival over harmattan spells of breeding-season adversity (why *M. bulocki* breeds at that season when other *Merops* species are rains nesters in a question probably best answered in terms of intra-generic competition; but that is at one remove from our present considerations). It would be extremely difficult to understand the evolution of a helper-class which thereby lowered its own productivity, were the helpers unrelated with the breeding pair which they assist. However, while we do have evidence of a low incidence of exogamy, most helpers undoubtedly originate within their colony, and at least some of them (probably the large majority) are the offspring by a previous mating of the parents they assist. Moreover, all of the evidence we have points to a pair of *M. bulocki* mating for life and having a high life expectancy, so that the coefficient of kinship between the donor and recipient of aid behaviour is 0.5, the closest kinship possible. Since we do not yet have the data enabling us to assert how (if at all) the lifetime fitness of a bird 'apprenticed' as a helper in its first year or two is thereby affected, we cannot label the act of helping in *M. bulocki* as altruistic or otherwise. Helpers certainly enhance the survival of the brood; they presumably alleviate marginally the parents' hardship, reducing the cost of breeding and increasing parental survival; and we think it likely that a helper's own lifetime fitness may also be increased by helping, because of the experience it gains when the only alternative to helping might be passing the season as a solitary 'non-breeder'. Almost certainly, helping serves to increase the commune's inclusive fitness.

In any event, the evolution of helpers seems to have been abetted by three further factors. The first, applying broadly to low-latitude landbirds, is high adult annual survival which might make it difficult for juvenile birds to enter the reproductive class. The second is a skewed sex ratio, despite *M. bulocki* being monogamous. How the numerical predominance of males in this species arises is still not known; we have some evidence that the earlier eggs in the clutch tend to be male and the later ones female, so that the greater mortality of younger than older nestlings means more males than females fledge. If there has been selection favouring a male-helper-class by means of the zygote-sex stratagem, its evolution would be a challenge to explain. The third is family cohesion. The period of dependence by fledglings on their parents and any helper lasts up to six weeks, and even after emancipation juveniles maintain bonds with the adults, and family groups roost gregariously throughout the non-breeding season. If a yearling bee-eater is unable to find a mate it has the option of remaining with its family and assisting in rearing the next brood. During the period of colonisation of the nesting cliff, bonds between helpers and adults are strengthened. Feeding of incubating females by helpers is commonplace, as well as 'courtship' feeding and mounting by them. 'Copulation' with the breeding female by a helper – her offspring – probably rarely if ever serves to inseminate her, but may serve simply in bonding, as among primates. During the nestling period only such bonded helpers are allowed by the breeding pair into the nest-chamber to feed young, others being aggressively driven away.

Merops pusillus

The Little Bee-eater *M. pusillus* is sympatric with *M. bulocki* and often occurs in the same habitats, sometimes nesting adjacently. It is a small bird (15 g), rather solitary,

somewhat migratory, and not markedly dissimilar to *M. bulocki* in diet, foraging behaviour or habitat. In northern Nigeria it breeds in April when the first rains are falling and May when rain is frequent. Even by April deciduous trees are well into leaf and flying insect life is evidently very abundant. Like all bee-eaters, it is single-brooded. It does not have helpers, despite having a much larger brood to fledge than has *M. bulocki* (mean clutch-sizes 4.4 and 2.9 respectively). We found 20 nests of *M. pusillus,* containing four or five well-grown nestlings within three to seven days of fledging, so that pairs are capable of fledging at least one more nestling than can be fledged by pairs of *M. bulocki.* Unaided pairs of *M. bulocki* can raise at most three nestlings, and only when helpers are present are broods of four successfully reared. It seems that during its breeding season *M. pusillus* does not normally encounter periods of food shortage long enough to endanger the survival of any of the brood. If that is in fact the case, we would expect it not to exert any selection pressure causing the species to depart from the avian norm of unaided monogamy. It is tempting to speculate that *M. pusillus,* being only 60 percent of the body weight of *M. bulocki,* might have a greater adult annual mortality (Lindstedt and Calder, 1976), so that juveniles have more openings available into the breeding community and the species is not thus predisposed to evolve helpers on that account either. However, many other tropical birds even smaller than *M. pusillus* are known to have excellent adult survival rates, and it may not be the case at all that in the genus *Merops* rates vary with body size.

Merops nubicus

Carmine bee-eaters *M. nubicus* are large (55 g), distant-foraging birds having much the same distribution as *M. bulocki* but being more riverine and less reliant on Hymenoptera. They feed on flying grasshoppers, bugs and beetles, often over a gram each. They breed in large colonies, starting about the same time as *M. pusillus.* Third adults sometimes make provisioning visits to a brood, but whether those adults are bonded helpers comparable to *M. bulocki* helpers has not been ascertained. An interesting difference between the three species is in the degree of egg-laying and hatching asynchrony (Table 1); in *M. pusillus* hatching is nearly sychronous, in *M. bulocki* at one-day intervals, and in *M. nubicus* at two-day intervals. It suggests that in that sequence the three species find it less easy to find plentiful food during egg production. That *M. nubicus* encounters difficulty thereafter in obtaining sufficient food is strongly suggested by Britton & Dowsett's (1969) analysis of weight losses sustained by breeding adults, and by our finding brood reduction in all nests studied. From any of eight clutches of two, no more than one bird fledged, while in broods of three the five-day interval between oldest and youngest nestlings meant that the latter had no chance at all of successfully competing with its siblings.

That *M. pusillus* can rear large broods unaided, at the same time and place where *M. nubicus* (despite some assistance) can raise only a proportion of its small broods, is presumably a correlate of diet prey size and quality in relation to the fact that *M. nubicus* is three to four times the weight of *M. pusillus. M. pusillus,* having higher annual productivity than *M. nubicus,* must have greater annual mortality (although whether of fledglings, juveniles or adults is unknown). If the mean annual adult survival of *M. nubicus* is superior, we would expect it to have helpers; we expect it to have helpers also from the premise that it has difficulty in finding enough food for its young. One explanation for the apparent paucity of helpers in *M. nubicus* is that while adult survival may be excellent,

fledgling mortality may be so high that very few first-year birds are availalble for recruitment as either helpers or breeders. The dilemma cannot be resolved until far more is learned about this species.

Merops albicollis

White-throated Bee-eaters nest in loose aggregations along the southern fringes of the Sahara, during the short season of sporadic rains at that latitude. After breeding they migrate gregariously up to 1300 km south and winter in lush, well-wooded habitats quite unlike the region in which they nest. The diet is more diverse than in any other *Merops* bee-eater, mostly small flying insects, but also small reptiles and even plant material (Fry, 1973). We have investigated only six nests, near Lake Chad, and most of them had plural helpers. One seemed to have no helpers. Most clutches were of six and there was no evidence of brood reduction (but we did not observe all young until fledging). One brood was being provisioned by a pair plus at least four helpers, mostly males. From the appearance of the breeding habitat one might think that *M. albicollis* is then faced with harsher conditions than any other West African bee-eater, but their fledging success suggests otherwise. The few available data lead to the prediction that this species will have excellent adult survival, high juvenile mortality compensated for by high reproductivity, yet a sufficient differential between reproductivity and gross annual mortality to produce a surplus the following breeding season (or seasons – helpers may well defer maturity for more than one year). In view of the unpredictability of rain and hence environmental productivity, the pool of helpers is expected to fluctuate from year and to function thereby in the social control of population density.

Without better data it is unwise to speculate about the preponderance of males.

Merops apiaster

This is the highest-latitude species and the only one that breeds exclusively outside the tropics. It winters mainly in southern Africa. The European Bee-eater's habitat is a variety of open country; it has a 'typical' diet of flying insects, mainly Hymenoptera and Odonata; and it breeds in medium colonies. We studied a colony in Hungary and found clutches up to nine eggs, a mean brood size of five, a high incidence of single helpers at nests, and a very high rate of provisioning. Broods were fed for 13 of the available 14 hours of daylight, at a rate often exceeding 50 food visits per hour; and at one nest attended by a trio of adults the greatest hourly feeding rate was 143. The temperate-zone summer favours high biotic productivity, and the bee-eaters exploit an abundant insect resource. The stratagem seems to be to utilise the summer flush of insects to maximise productivity of young (Lack's hypothesis). Doubtless the species often has to endure weather that depresses the availability of its food, and the presence of a helper may then partly offset any brood reduction. For this bee-eater the most crucial event in the annual cycle is the trans-Saharan migration into Africa; migrant mortality is known to be high, and is probably particularly so amongst naive juveniles. Helpers may improve not so much survival to fledging as the condition of fledglings, perhaps giving them a selective advantage during migration over fledglings from unassisted nests.

Conclusion

The degree of helping behaviour in *Merops* spp. does not correlate consistently with any one of the generic variables listed in Table 1. But for each species those variables will interact to produce a characteristic survival curve, and all the evidence points to the bee-eaters differing markedly in specific survival patterns. That results in large part from seasonal and demographic differences in the operation of the chief mortality factors encountered by each species. All bird species having long-term population stability must produce either sufficient young exactly to match that year's adult loss, or a surplus of young in better years to offset deficient production in poorer years. The first alternative will be very rare. This means that in nearly all species there must be a temporary surplus in many years – as studies of temperate-zone passerines have shown, the surplus being a non-breeding population in the breeding season. If the excess of first-year survivors over breeders' annual mortality occurs in a majority of years; and if the social character of the species permits the excess of non-breeders to be socially included rather than excluded; and if, moreover, a selective advantage accrues to all social classes concerned, then the result must be the helping phenomenon.

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To Skew or not to Skew?

Sandra L. Vehrencamp

Introduction

Not only is the roster of cooperatively nesting avian species increasing rapidly, but the variety of group-breeding strategies is also large. Recent work on the evolution of cooperative nesting has focused on explaining the advantages of group breeding over single-pair breeding. However, no attempt has been made to understand why one form of cooperative nesting evolves over another. The single most important factor which differentiates many types of cooperative systems is the degree to which reproduction and parental effort are shared or skewed among the members of a group. In fact, cooperative systems could be placed along a continuum of increasing skew in reproductive success. Ostriches (Sauer & Sauer, 1966), pukekos (Craig, 1974), magpie geese (Frith & Davies, 1961), and anis (Vehrencamp, 1977) are some examples of group nesters with no or very little skew, since all the females in a breeding group lay eggs in the communal nest. An intermediate level of skew occurs in the Tasmanian hen (Ridpath, 1972), where one male of a trio copulates with the female about two times more frequently than the other male. Helper-at-the-nest species such as jays and many others (see Brown, 1978) exhibit a very large skew, with one pair producing all of the offspring and all other group members contributing only to the care of these young. Since low-skew cooperative groups do exist, the question arises: Why don't the helpers at the nest breed along with the dominant pair? To understand the evolution of cooperative nesting, we not only need to know why groups form, but also how much skew in reproductive success can be generated. In other words, the alternate strategies to helping are not only leaving to breed alone but also breeding cooperatively with lower degrees of skew. Here I shall assume that group formation is advantageous, and examine the factors which determine the amount of skew.

Skew is defined as differences in the fitness of group members of the same sex which are the result of dominance interactions. Differences in reproductive success due to chance factors and age-specific reproductive capacities are not included. Fitness, hereafter designated by W, is measured as the number of young produced times the probability of survival, and thus both offspring production and risk-taking may be skewed in a cooperative group. Fitness could be calculated on a per nest basis, but lifetime fitness (net reproductive rate) is preferable.

The model

I have worked up a simple model which clarifies some of the factors involved in domination and which defines the maximum amount of skew which a dominant can demand from a subordinate. There are several necessary conditions which must be met for my model to apply. These are:

(1) that group living and/or cooperative nesting confers some overall benefit to all group members compared to solitary pair breeding. Specifically, the mean fitness of all group

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members ($\bar{W}$ = total combined fitness of the group, divided by the number of birds in the group) is greater than solitary breeding (W_1). I assume that $\bar{W}$ first increases with increasing group size, plateaus at some optimal group size, then declines with larger group sizes.

(2) that dominance hierarchies will form once groups form.

(3) that dominants will try to skew the reproductive success in their favour as much as possible. Selection on dominants to dominate will occur as long as the benefits of dominating outweigh the costs.

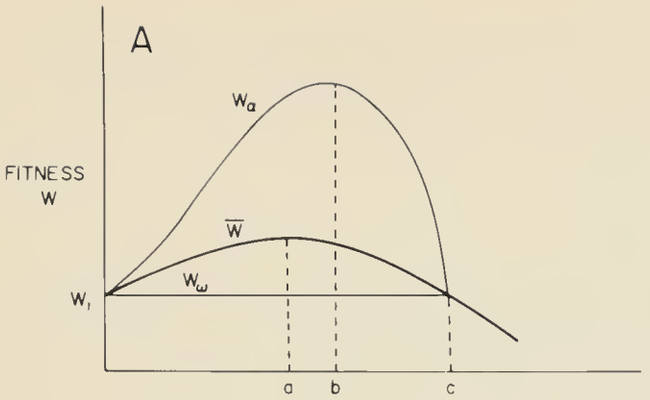
(4) that the ultimate defence of the subordinate against domination and skewing is to leave the group. Subordinates will leave when their fitness in the group goes below what their fitness would be as solitary breeders, devalued by the costs of dispersal. Since it is to the advantage of the dominant to maintain the group, it should only skew to the point where the subordinate's fitness in the group is equal to or slightly better than a solitary breeder.

(5) that for every unit of fitness by which the dominant can reduce the reproductive success of a subordinate, the dominant's fitness increases one unit. For example, if the dominant can prevent each subordinate from laying one egg, then the dominant can usurp the subordinate's parental potential and produce one more of its own offspring for each subordinate in the group. Units of survival can be skewed in the same way. In other words, there is a fixed output for the group equal to $\bar{W}$ times the group size, and the fraction of this that belongs to subordinates and dominants changes with differing degrees of skew.

(6) that all subordinates are skewed by the same amount, and that there is only one dominant in the group.

I shall consider two cases. First, take the simplest case of a group of unrelated animals. The maximum amount of skew in reproductive success which can be generated is illustrated in Figure I A. I have assumed that the average fitness $\bar{W}$ increases to a peak, then declines with increasing group size. W_1 is the fitness of a solitary individual or pair, and a horizontal line intersecting W_1 is W_ω, the lowest point that the dominant can push the fitness of subordinates. The dominant's enhanced fitness is then calculated from these two lines and is the difference between $\bar{W}$ and W_ω times the number of subordinates, or $W\rightleftarrows = \bar{W} + (\bar{W} - W\omega)(k - 1)$, where k = group size. The greater the difference in reproductive success for groups and solitary individuals, the greater the skew can be. If $\bar{W}$ is equal to W_1, as at the group size c, groups without skew might form. Where $\bar{W}$ is less than W_1, no groups can form. Notice that the optimum group size which a dominant would prefer (b) may not be the same as the optimum group size of a non-skewed group (a).

For the second case in which the individuals in a cooperative group are related by some mean coefficient of relatedness r, the model is altered so that subordinates leave the group only when their inclusive fitness in the group falls below what their inclusive fitness would be if all the group members bred solitarily (see VEHRENCAMP, 1978). Figure I B illustrates the maximum amount of skew in personal fitness that could be demanded by the dominant relative. I have used the same $\bar{W}$ line as in the previous case, but here the group members are related by an r of .25. The subordinate's personal fitness is line W_ω ; each point along this line represents equal inclusive fitness for the group situation and the solitary strategy.



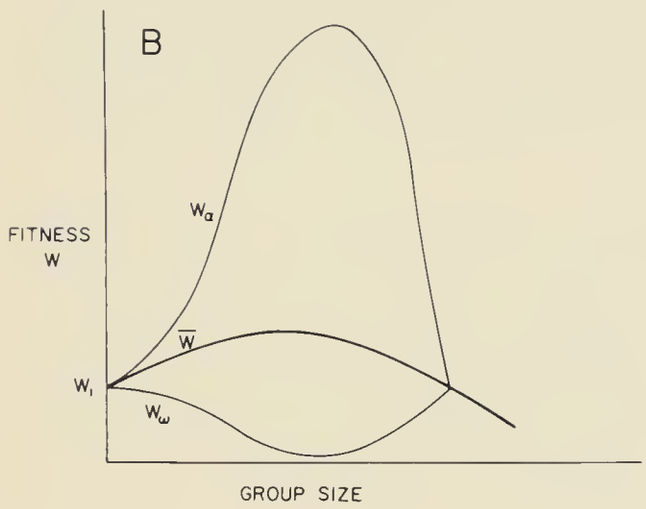


Figure 1. The maximum amount of skew which can be generated between dominants and subordinates in groups containing (A) unrelated animals, and (B) individuals related by $r = 1/4$. $\bar{W}$ is the average fitness of a group member, W_α is the fitness of the dominant, and W_ω is the fitness of subordinates.

For the case of related individuals, therefore, W_ω can go below W_1, and the greater the degree of relatedness, the lower W_ω can be pushed. W_ω can even be pushed to zero among close relatives, depending once again on the difference between $\bar{W}$ and W_1. The fitness of the dominant is calculated in the same way as before. Because the difference between $\bar{W}$ and W_ω is greater, the dominant gains a rather large benefit, and the skew in this case is very great. One of the most interesting predictions of this model is that even among close relatives, the dominant cannot manipulate subordinates and force group formation unless the average personal fitness of group members, $\bar{W}$, is greater than the personal fitness derived from solitary breeding, W_1. Parental manipulation of offspring is a special case of this model. The fitness of some offspring is reduced in order to produce more total offspring. The equations require a correction factor to account for the cost to the parent of producing the initial set of helpers. If this cost is great, it has the effect of reducing the amount of skew the parent can demand.

Summarizing the two models, dominants are limited in their ability to dominate by the degree to which opportunities for breeding outside the group are available to subordinates. The lower the success of breeding solitarily, the greater is the skew which the dominant can impose. The model predicts that the fitness of subordinates in a group should be equal to or slightly better than its fitness as a solitary. In the case of related group members, however, inclusive fitness determines the criterion for leaving. Since subordinates are related to the dominant's offspring, the dominant can impose more skew in personal fitness on subordinates before inclusive fitness in the group is lower than the inclusive

fitness of solitary breeding. The closer the relatedness, the greater the skew in personal fitness the dominant can demand. However, for both unrelated and related group members, neither groups nor skew can be generated unless $\bar{W} > W_1$.

Factors affecting the amount of skew

Several questions follow from the model. The most obvious is: What determines whether groups contain relatives or not? Let us take the point of view of a dominant individual trying to decide whether to recruit relatives or non-relatives as subordinates into its group, and whether or not to skew them to the maximum allowable. Using straightforward equations for inclusive fitness, I have compared the relative success of these options (see VEHRENCAMP, 1978). Given that $\bar{W} > W_1$, skewing is always better than not skewing. But whether to skew relatives or non-relatives is a complicated issue and depends on two factors: (1) the magnitude of the difference in reproductive success of groups and pairs, and (2) the probability of successful dispersal. These two factors are components of lifetime fitness, such that $W = s \cdot R$ (s = the probability of dispersing successfully, and R = total output of young after successful dispersal). Holding all other variables constant, and increasing the relative reproductive success of groups ($\bar{R}/R^1$), the optimal strategy changes from recruiting and skewing kin when the group benefit is small, to dispersing kin and skewing non-kin when the advantage of grouping is large. The reason for this reversal of strategies is because for large group benefits, the advantage gained by the dominant in allowing the kin to breed in low skew non-kin groups (where some may even be dominant) far outweighs the loss of skewing only non-kin.

The probability of successful dispersal, s, is particularly relevant to the case of parental manipulation of young, since s is only applied to the individual which leaves the kin group in which it was born. Holding all else constant and varying s between 0 and 1 also leads to shifts in the optimal dispersal strategy. If dispersal survival is high, a parent (or dominant relative) gains by dispersing its offspring (kin). The lower the probability of dispersing successfully, the greater the advantage gained from retaining and skewing the offspring (kin). Dispersal survival is most important for territorial species, where leaving the parental territory can entail great risks for the disperser. For non-territorial colonial species, young need not "disperse" to breed solitarily in the parental colony. Thus for these species (e.g., bee-eaters), the magnitude of survival and reproductive advantages in groups is the main factor affecting group composition and skew.

Dispersal survival and the relative advantage of grouping over solitary breeding interact in complicated ways to determine whether kin or non-kin groups should form. When s is high and $\bar{R}$ is much greater than R_1, non-kin groups should form. When s is low and $\bar{R}$ is not much larger than R_1, kin groups should form. The other mixed possibilities depend on the relative values of s and $\bar{R}/R_1$, and we are currently developing a quantitative model to predict these strategies.

One final question arises from the model: Is the dominant always able to skew the reproduction to the predicted maximum? The skew may be less than predicted for several reasons. (1) If the skew is less than predicted for the case of related animals but not for unrelated animals, then we might suspect some problem with kin theory, for which this model is a test. If the skew is less for both related and unrelated groups, then one of the

following explanations may be applicable. (2) If the cost of parental care is small compared to the cost of eggs, then it may not be worth skewing. For instance, helper-at-the-nest systems in birds occur only among species with altricial young or precocial young which require feeding. Self-feeding precocial species do not exhibit helping, and where grouping is advantageous, the skew is low (ostriches, magpie geese). (3) The dominant may not have the opportunity to skew the reproduction. For example, in rheas females may attempt to roll eggs out of the nest but are usually prevented from doing so by the parental male (BRUNING, 1974). (4) Subordinates may have effective strategies for reducing the skew. In the anis, subordinate females have adopted three strategies for reducing the skew caused by the dominant female's egg tossing (see VEHRENCAMP, 1977). (5) Hormonally, animals may have to breed before they can perform parental care. This may explain why helpers don't incubate, and why helping in mammals is vary rare. (6) Finally, behavioural domination may be too costly in terms of time and energy. For example, if the optimal group size is very large, the dominant may not be able to effectively control all of the subordinates.

Are the data consistent with the model?

How do existing data support the model? Survival and lifetime fitness are rarely determined for cooperative nesting species, but for birds in general, high-skew helper systems occur among closely related individuals, and low-skew cooperation among unrelated individuals. Data on anis support well the case for unrelated group members (VEHRENCAMP, 1979). Groups of two to three pairs form largely in the optimal, high density habitat, but dispersing birds have available to them vast areas of suboptimal breeding habitat. Thus all females disperse from their parental groups. In the optimal area, groups of two to three pairs are slightly more successful than single pairs, and a small skew in egg ownership is generated by the dominant's egg-tossing. The fitness curve for subordinates in groups forms a very nearly straight horizontal line with W_1, as predicted by the model.

To illustrate the case of related group members, If have avoided presenting an avian helper species, and instead present the excellent data of METCALF & WHITT (1977) on a facultatively social wasp, *Polistes metricus*. The wasp has two advantages: (1) it breeds only one year so lifetime fitness is easy to determine, and (2) the cooperating relatives are sisters, which makes calculations easier than for the parent/offspring situation. $\bar{W}$ for two-female groups is higher than W_1, but the skew in offspring production is high, 82% – 18%. The beta female's personal fitness is about half that of a solitary female. However, inclusive fitness for the beta female is slightly higher in the group than if both sisters bred solitarily, again supporting the model.

Conclusions

In conclusion, the model seems to rest on quite reasonable assumptions and is consistent with available data. I believe we shall soon have enough information to test the model with an avian helper-at-the-nest species, although some refinements of the model may be required. The application of helpers-at-the-nest to the model may even lend insight into the problem of parent-offspring conflict as outlined by TRIVERS (1974) and ALEXANDER (1974). Regardless of the final model, my basic point will stand: that is, given the

perspective of a range of skew in cooperative nesters, the fact that helpers could be breeding must be included as a cost to the helper along with the costs of guarding, feeding, etc. Teasing out the environmental factors which shift these costs, and thus the skew, is as much a challenge as explaining group breeding in the first place.

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Systems and Strategies of Communal Breeding in Australian Birds

Douglas D. Dow

Introduction

In the earliest account of an Australian species, the Superb Blue Wren *Malurus cyaneus*, Rowley (1957, 1965a) suggested that its communal breeding permitted an increase in reproductive output when food was abundant, and introduced the view that communal breeding was thus an adaptation to the erratic climate of Australia. Other communally breeding species have since been identified and a few studied. Rowley's now general interpretation of the adaptive value of the behaviour has been echoed (Harrison, 1969; Rowley, 1976).

I think, however, that prevailing opinions on the influence of Australian climatic patterns have suffered too long from over-generalization. The view that most communally breeding birds live where rainfall and thus food is most erratic is clearly wrong. Australia has a wide variety of vegetation and thus habitat types. Ornithologists working in the east have commented on the stable rather than erratic nature of the environment there (Kikkawa, 1968; Dow, 1970; Ridpath, 1972c; Parry, 1973).

Rowley (1976) included 39 species in his review. I have expanded that list to 57, but where publication of breeding habits is so sparse, it is difficult to assess how regular communal breeding may be in some of these. Details and documentation of these species can be found in Dow (in press a).

In keeping with a descriptive terminology, the term 'helper' is not used in that or this paper. The following terms are more fully discussed in Dow (1979). *Group:* A socially discrete unit usually composed of a primary pair and secondary individuals. *Flock:* A discrete assemblage in time and space that may include some or all members of one or more groups. *Attendant:* A general term denoting any bird at a nest or feeding fledglings. *Auxiliary:* Any attendant that is also a secondary member of the group. *Complement:* A collective term for the primary male and all auxiliaries attending a particular nest or brood.

Social systems

Social systems are conceptual models to aid comprehension and communication of biological organization. They cannot be absolute and must reflect, often arbitrarily, the attitude of the investigator. For communal breeders we can usefully describe aspects of social systems by using the nest as our point of reference. This permits the incorporation of fragmentary data. Description at this level is outlined in Table 1.

With a single nest, an observer could obtain additional information on the kind of social system to which initial observations belong: I. What is the size of the complement? J. Are members of the complement also attending other nests? K. Do attendants belong to a single, normally integrated group? L. Is the group territorial or spatially discrete from others? M. Are fledglings, i.e. dependent young, present in the group? N. What is the sex

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TABLE 1: Descriptive Parameters of Social Systems of Communal Breeders, using the Nest as a Point of Reference

A_1 single female laying
A_2 more than one female sharing the nest
B_1 other females nesting close by
B_2 no other close nests
C_1 third attendant only
C_2 more than one auxiliary
D_1 auxiliaries feed primary female
D_2 auxiliaries do not feed primary female
E_1 auxiliaries participate in building
E_2 auxiliaries attend without building
E_3 auxiliaries do not attend during building
F_1 auxiliaries participate in incubating
F_2 auxiliaries attend without incubating
F_3 auxiliaries do not attend during incubation
G_1 auxiliaries feed nestlings
G_2 auxiliaries attend without feeding nestlings
G_3 auxiliaries do not attend nestlings
H_1 auxiliaries feed fledglings
H_2 auxiliaries attend without feeding fledglings
H_3 auxiliaries do not attend fledglings

ratio of the group (or complement)? Longer-term observations would go further in describing a social system.

Many of the species studied in detail diverge sufficiently to be classed as different systems. I identify seven such systems by the generic name of species showing them. Space permits only the briefest description of differences among these systems (Table 2). Further

TABLE 2: Abbreviated Summary of the seven Best-Known Australian Communal Breeding Systems

	Females share nest	Other nests nearby	Commonly nest as simple pair	Usually more than one auxiliary	Auxiliaries regularly feed primary female	Auxiliaries incubate	Auxiliaries build	Auxiliaries feed nestlings	Auxiliaries feed fledglings
Dacelo	−	−	+	+	−	+	−	+	+
Tribonyx	−	−	+	−	−	+	+		+
Malurus	−	−	+	+	−	−	−	+	+
Acanthiza	−	?	+	?	−	−	−	+	+
Pomatostomus	o	−	−	+	+	−	+	+	+
Corcorax	o	−	−	+	?	+	+	+	+
Manorina	−	+	−	+	−	−	−	+	+

(+) do so regularly (−) not regularly (o) do so rarely

details can be found in the following: *Dacelo* (Parry, 1971, 1973); *Tribonyx* (Ridpath, 1972a, 1972b, 1972c; Smith & Ridpath, 1972); *Malurus* (Rowley, 1957, 1965a); *Acanthiza* (Immelmann, 1960; Ford, 1963); *Corcorax* (Rowley, 1965b, 1976); *Manorina* (Dow, 1970, 1975, 1977, 1978a, 1979, in press; Swainson, 1970). *Pomatostomus* (King, 1974, 1975; Counsilman, 1975, 1977; Brown et al., in press; Brown & Dow, unpublished).

It is significant that the first seven species of communal breeders examined in Australia show such diversity of systems (Table 2). The two non-passerines differ from the passerines in their high incidence of nesting as simple pairs, in that auxiliaries share in the building of the nest, and that all attendants incubate. In all systems, auxiliaries show strong parental-like behaviour in feeding nestlings and fledglings, not surprising as this is a virtual definition of communal breeding.

In some of the passerines, group-living and communal breeding appear almost obligate; *Malurus* and *Acanthiza* are the only ones showing frequent nesting as simple pairs. *Manorina* is unusual in its colonial organization and the sharing of many nests by many males. *Corcorax* is the only passerine system in which incubation may be shared with the primary female, and it and *Pomatostomus* are the only two in which nest building is a communal activity. This could be an adaptation with possibly little relevance to communal breeding per se in *Pomatostomus*, as group members roost together year-round in a domed nest. Nest building continues throughout the year with many or all members of the group participating. Nests are large, bulky structures requiring much material. As auxiliaries become proficient in nest building, it may be to the advantage of the primary female to permit them to build. *Corcorax*, on the other hand, builds a mud nest. The effort to build a large nest might be considerable and the conditions not always appropriate. That many old nests are renovated (Rowley, 1965b) supports this view. By having several birds participate perhaps ensures that when mud is available for only a short time it can be utilized efficiently.

Strategies of reproduction in communal breeders

Postulated strategies of animals are inherently anthropocentric. Before a strategy can be discussed, a goal must be specified. Communal breeding has been interpreted as a strategy permitting species to maximize their reproductive output. Evidence does not support this view, nor has any experimental or comparative field study been done to test it. In no Australian communal breeder have auxiliaries been shown to substantially increase annual production of young over that found in simple pairs. Unless auxiliaries are all males or are sexually immature females, not usually the case, annual productivity in a population would be increased by having more females nesting.

Rather, I have been impressed that reproductive success of communal breeders is not higher: *Tribonyx*, 55% survived per clutch over four months (Ridpath, 1972b); *Dacelo*, 1.8 fledglings per nesting female (Parry, 1973); *Acanthiza*, 63% of nests fledged some young (Ford, 1963); *Malurus*, 64 nests produced 58 fledglings (Rowley, 1965a); *Manorina*, nest success less than 17% in each of three years (Dow, 1978a); *Pomatostomus*, nest success 32% in one year (Counsilman in Dow, 1978a). Studies may have been made when available resources were not at their best, but they do suggest

that a major strategy may be the lowering of reproductive effort through life. Communal breeders in Australia, perhaps many species there, may be long lived (Rowley, 1965a; Parry, 1973; Boehm, 1974; Morris, 1971, 1975; Lane, 1976). Longevity permits a more leisurely approach to reproduction if the goal is simply on average to replace individuals from generation to generation. Perhaps a single productive year in the life of a breeding individual will suffice. But rather than being programmed to breed only in good years, an individual could reduce its effort generally. Thus the conflict between personal survival and the risk of breeding will be reduced. Auxiliaries provide a breeder with the means to reduce effort through feeding its young. In most Australian communal breeding systems some adults do not breed. Adult rather than juvenile auxiliaries as in *Acanthiza* and *Malurus* are usual. In some studies, females known to have nested in a previous year made no attempt (*Manorina:* Dow, 1978a).

If nesting and breeding behaviour in general place the primary female or pair at greater than usual risk of predation and if the environment is one that permits or induces longevity, then selection for intensive or frequent breeding effort may be much less than for birds of high latitudes on other continents. The reduced clutch sizes of Australian birds, which surprise some authors (Courtney & Marchant, 1971) because Australia is in large not tropical, may well be a general expression of reduced reproductive effort concomitant with increased longevity and decreased migration. Communal breeding should reduce in the primary pair the physiological strain of provisioning a brood. Evidence suggests that this is the case (Parry, 1973; Brown et al., in press; Dow, 1978b). It may be that in climatically good years, the cost of attempting subsequent broods is lowered sufficiently for the primary female by auxiliaries' efforts, as is suggested by correlations between annual productivity and group size (Rowley, 1965a; Parry, 1973; Brown & Dow, unpublished).

For the auxiliary, the risk of reproduction, particulary in the early inexperienced years, is minimized through participating as only one of several attendants to highly conspicuous offspring at the nest or other site. That risk is further minimized by extending the role of auxiliary into later life. Male auxiliaries in some systems may occasionally have the chance of fertilizing a primary female. Thus to attend a nest as an adult auxiliary is also part of the strategy of reducing reproductive effort. Presumably experience lowers the cost of reproduction and lifetime output can become high. Also, a genetic gain might result if, while reducing reproductive effort by becoming an auxiliary, the individual associates with its close kin.

Factors promoting communal breeding

Lack (1968), in summarising predisposing factors, suggested (1) young staying with parents through the non-breeding season, (2) marked surpluses of males and (3) reduced migration in Australia. However, the sex ratio in at least half of those communal breeders studied is equal and in some of the others could be a result rather than a cause of the behaviour. Harrison (1969) thought that 'some common underlying factor' must be involved and suggested climate, in particular aridity. But most studies have been made of species living under conditions prevailing in the eastern part of the continent, not under arid conditions. Indeed, some writers have remarked on the equable nature of the regions where their studies were made (Dow, 1970; Ridpath, 1972c; Parry, 1973).

Rowley (1976) stated that the 'one common denominator' was the persistence of young in families and that under Australian conditions the pressure to be quickly rid of young would not be great. His conclusion remained that communal breeding is an adaptation to irregular climate in enabling maximum reproductive effort to be made when favourable conditions permit.

A weakness of this interpretation lies in its implication that many species must be living under much more regular and favourable climatic conditions than these communal breeders. If theirs are just the conditions that enable maximum reproductive effort through breeding communally, why do most species chronically enjoying the opportunity not indulge in the habit?

I think it likely that previous discussions have erred in emphasising erratic climate or in seeking a single underlying ecological factor. The systems of Australian communal breeders are now known to be diverse and complex, thus precluding simplistic explanation. No obvious patterns of communal breeding emerge when considering distribution in ecogeographic zones or vegetation types. I think it important to see the habit as a social as well as an ecological phenomenon. We define communal breeding by the observation of birds feeding others, yet the literature abounds with examples testifying to the almost overpowering social stimulus of the soliciting displays and actions of young birds. The evolutionary consequences of the intense competition among nestlings and fledglings in stimulating parental attention O'Brien & Dow, 1979) have not received adequate discussion in the context of communal breeding. Examples of interspecific feeding at nests are dismissed as aberrant. The strongly stimulating behaviour of young cuckoos is well known. Kikkawa & Dwyer (1962) record three species feeding a fledgling Pallid Cuckoo *Cuculus pallidus* in eastern Australia (see also Hardy & Hardy, 1973). Welty (1962) describes, complete with photograph, an American Cardinal *Richmondena cardinalis* feeding a gaping goldfish. Any situation enabling individuals to be close to begging young should be predicted as one in which such behaviour will arise. Thus, the proximate or predisposing factors to communal feeding, I would argue, are strictly social: (1) The opportunity for frequent and long-term social contacts through which familiarity and tolerance are increased, and (2) the sharing of a group territory or home range.

The way these factors inter-relate is shown in Figure 1. I contend that communal breeding has arisen a great many times initially through social accident in stable rather than erratic climates. The same ongoing opportunities will help maintain the habit. Where this behaviour is ultimately of significant advantage to all participants, a communal breeding system appropriate to that species in conjunction with other social and environmental pressures will evolve.

Nomadic forms are included in Figure 1. Nomadism among Australian birds has probably evolved in response to erratic rainfall in arid regions (Davies, 1976). Nomadic populations travelling in flocks retain the social advantages of increased efficiency in foraging and protection as well as the opportunity for frequent social contact. They may lack the advantages of familiarity with a small home range, but socially would be equivalent to sedentary birds.

However, it is in equable climates that we would expect both reduced migration and reduced fluctuation in resources. The model (Figure 1) indicates that a reduction in migration and a stabilization of resources should permit reduced dispersal and increased

longevity, both of which will increase opportunity for long-term social contacts. Such contacts, particularly in a species in which individuals' ranges overlap in a group home range or territory, will increase the tolerance of adults to an individual approaching their nest or young.

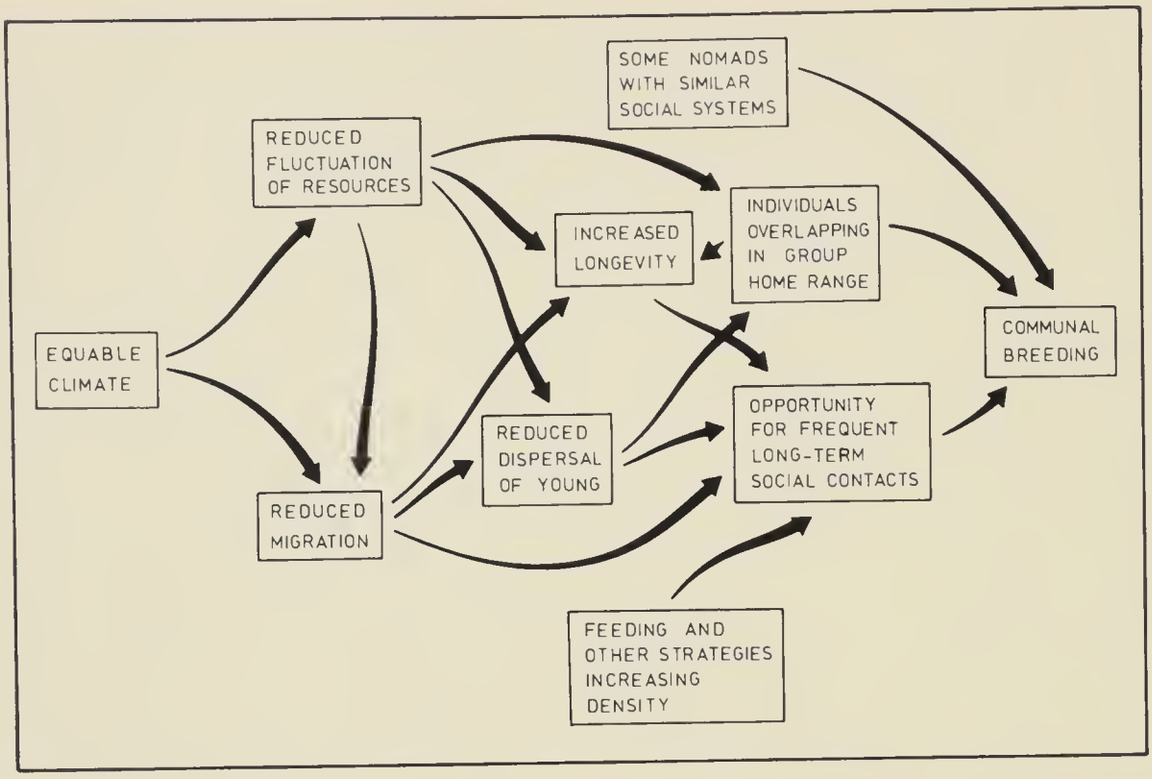

FIGURE 1. A model of the interaction of factors promoting communal breeding among Australian birds. See text for details.

The parental-like responses of birds living under such conditions would be frequent because they would be in close proximity to the nests and offspring of familiar individuals and in many cases reciprocal familiarity would lead to their acceptance by the breeders.

The examples given by SKUTCH (1961) of interspecific attendants could be expanded greatly, and although there is no genetic connection between participants, the behaviour far from being 'aberrant' seems quite natural and indeed the donor could conceivably benefit through the experience as has been suggested by some writers for intraspecific auxiliaries.

From current knowledge about the social systems of Australian communal breeders I think it reasonable to conclude that the phylogenetic diversity shown by the well-documented examples negates the possibility of a few major lines of evolution. Observations of occasional auxiliaries at nests of some species support this view as well as the thesis that communal feeding is a frequent and spontaneously generated social habit.

I have dealt mainly with proximate social factors conducive to communal breeding. Because the Australian environment would seem to promote these types of sociality and because communal care of young should thus arise spontaneously, the evolutionary significance of reported communal breeding in many species might be questioned. Some birds, e.g. *Malurus*, appear to be socially opportunistic in breeding communally from year to year. In others, e.g. *Manorina* and *Corcorax*, communal breeding appears obligate. It is

among these obligate communal breeders that ultimate factors underlying the behaviour must be sought.

Available studies indicate the variety of systems that have evolved. We await detailed comparative studies within genera where communal breeding is widespread, e.g. *Malurus, Manorina, Melithreptus, Artamus* and probably *Pomatostomus,* for insight into how particular evolutionary lines may have been modified under conflicting ecological and social constraints.

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Pair Territories and Group Territories – The Nature of the Adaptive Landscape

Anthony J. Gaston

It is a fundamental posthulate of sociobiology, as defined by Wilson (1975), that if we can completely understand the ecology of a species we should be able to predict its social behaviour. In practical terms, however, this has proved difficult to substantiate. Comparing pair and group territoriality among birds during the breeding season, a broad generalization can be made that group territories are mainly found in warm-temperature, sub-tropical and tropical climates, but otherwise ecological correlates of this behaviour appear to be difficult to define (Grimes, 1976; Rowley, 1976; Woolfenden, 1976; Zahavi, 1976). In some areas pair and group territorial species of similar morphology, and occupying apparently similar niches, occur side by side. An example can be found in the moist-deciduous and semi-evergreen forests of South India, where pair territorial species of *Turdus*, *Zoothera* and *Pomatorhinus* co-exist with group territorial species of *Turdoides* and *Garrulax* (pers. obs.). All the members of these genera are medium sized passerines, weighing from 60 to 120g, feeding on the ground, particularly among leaf litter, and having largely insectivorous diets, supplemented by fruits, seeds and nectar (Ali, 1967; Ali & Ripley 1971; pers. obs.).

I intend to examine some features of adaptation to group territoriality which suggest that a mixture of strategies can be expected in certain circumstances. In referring to group territorial behaviour I am basing my consideration on the type of behaviour found in *Turdoides* (Zahavi, 1974; Gaston, 1977, 1978), which appears to be typical of many group territorial species.

The initial transition from pair to group territory apparently begins with adaptations which increase the tolerance of territory holders towards conspecifics (usually their own offspring) within their territory (Gaston, 1978a). Once groups become established the evolution of behaviour which is adaptive in a group context is to be expected, including a system of sentinel behaviour for the detection of predators and also communal nest defence. The close degree of relatedness among group members means that kin-selection is likely to influence the evolution of behaviour (Brown, 1974) and this might be particularly important in the case of sentinel behaviour. Behavioural adaptations may also involve changes in, or extensions of, the feeding niche and these could be followed by morphological adaptations. Ultimately it is possible that reliance on sentinels for the detection of predators might broaden the choice of nest sites to include sites which are less cryptic than those formerly chosen. As these adaptations proceed they will tend to intensify the selection pressure towards adopting group, rather than pair territoriality.

The directional component in the evolution of group territorial behaviour is likely to be particularly strong because of what I have termed the 'patrimony factor' (Gaston, 1978a). Group territoriality probably arises in situations where a shortage of vacant territories encourages young birds to remain in the parental territory for one or more seasons. If competitiveness increases with age, a bird adopting this strategy should have an advantage

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over birds leaving the parental territory earlier. Once most of the population are deferring their dispersal from the natal territory, however, the chance of securing a vacant territory is much reduced, because most territories will already contain birds which can succeed to their ownership in the event of the demise of the holder. In this way a self-reinforcing feedback cycle is established similar to that proposed by SOUTHWOOD (1976) for adaptations occurring in response to K-selection.

The adoption of group, rather than pair-territorial behaviour, is probably dependent on a combination of ecological parameters, including those affecting adult survival, reproductive rate, dispersal, type of food and feeding strategy (BROWN, 1975; RICKLEFS, 1975; GASTON, 1978a). To simplify matters I designate the combination of environmental variables which determine these parameters for a particular species the 'group pressure' (G) on the species/population. G is likely to vary between different parts of the species' range, depending on the variation of its components such as environmental stability, resource levels and constancy. The threshold value of G, above which individuals of a pair territorial species begin to adopt group territories, is defined as the value of G at the point where

$$F_g/F_p = 1 \ (G_O)$$

where F_g is the fitness of an individual adopting a group territorial strategy and F_p is the fitness of an individual adopting a pair territorial strategy. The value of G at this threshold is designated G_O. The process of adaptation to group territoriality should result in a lowering of this threshold value for G, so that after time t_1 it becomes G_1, where $G_O > G_1$. To look at the process in another way, we can expect that in an unchanging environment (G constant) F_g/F_p should be positively correlated with the length of time elapsing since the species adopted group territoriality.

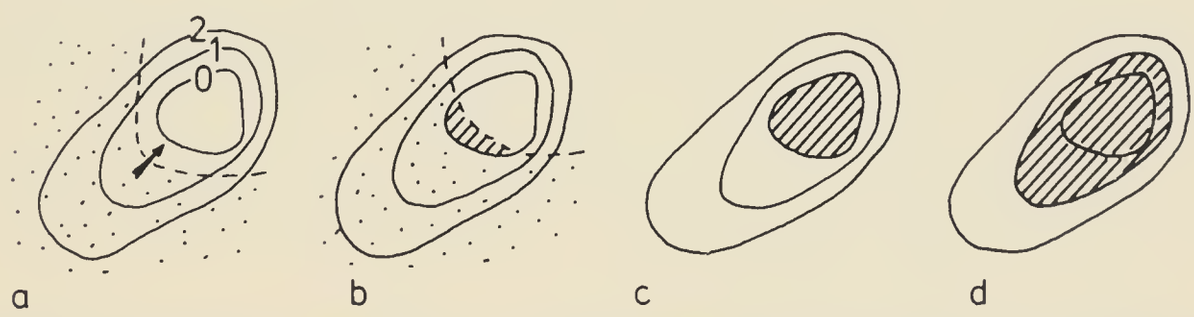

FIGURE 1. Schematic representation of a species extending its range into an area where there is selection for group territorial behaviour. Dotted areas = pair territories; diagonally shaded areas =group territories. For further explanation, see the text.

If we envisage a map on which the values of G for the species are plotted as contours (Figure 1), then the contour G_O defines the area within which the evolution of group territorial behaviour will be selected for. A species extending its range into this area should begin to adopt group territories once its population density approaches the carrying capacity of the habitat (Figure 1b). After t_1 the process of adaptation should allow the group territorial population to expand to the area bounded by contour G_1 (Figure 1d). In the area between the contours G_O and G_1 we can expect the co-existence of the group territorial population with pair territorial species of similar ecology.

The co-existence of group and pair territorial species of similar ecology can thus be explained in terms of their distributional history, group territorial species colonising the area down a gradient of decreasing G and pair territorial species spreading in the opposite direction. An examination of the above mentioned genera co-existing in the forests of South India provides some evidence for this hypothesis.

The group territorial genus *Turdoides* is typical of semiarid scrub and dry deciduous woodland over a large part of Africa and southern Asia (Ali & Ripley, 1971). This type of habitat appears to provide the optimum conditions for the evolution of group territorial behaviour (Grimes, 1976; Brown, 1978; Fry, 1977; Gaston, 1978a), and the two species of *Turdoides* found in moist deciduous and semi-evergreen forests in South India (*T. striatus and T. subrufus*) probably derived originally from populations in drier, more seasonal environments. In contrast, the pair territorial genera *Turdus, Zoothera* and *Pomatorhinus* are confined to moist forest habitats throughout their range (Ali & Ripley, 1971, 1972). The group territorial genus *Garrulax* is also confined to moist forest, but populations in the forests of South India almost certainly derived from populations occupying the middle-altitude forests of the Himalayas during the Pleistocene (Ali, 1935, 1948). The latter area is particularly rich in group territorial genera (*Yuhina* – Yamashina, 1938; *Aegithalos* – Nakamura, 1972; *Garrulax* and probably many other genera of Timaliinae – pers. obs.) and may therefore, like the lowland deciduous forest, represent an area where G is high for many species of passerines.

It appears that adaptations to group territorial behaviour, while increasing F_g, may also lower F_p. An individual of a pair territorial species can switch to group territoriality without loss of fitness in terms of its pre-existing reproductive and feeding behaviour (this might not apply to certain feeding strategies), but an individual of a group territorial species which adopts a pair territorial strategy may suffer from adaptations to feeding, predator detection and nest-site selection which reduce its fitness in a pair territory. Species of *Turdoides* which feed away from cover, for instance, such as *T. squamiceps* and *T.malcolmi,* are virtually dependent on the presence of sentinels to alert them to the presence of predators. Because of the patrimony factor it seems unlikely that strategies intermediate between pair and group territories constitute 'evolutionarily stable strategies' (Maynard Smith, 1975) and the adoption of group territorial behaviour may thus constitute an evolutionary one-way street.

Several authors have regarded group territorial behaviour as the result of K-selection, since it normally involves deferred maturity, high parental investment, reduced per capita reproductive rate and a stable population (Brown, 1974; Wilson, 1975; Gaston, 1978a). It is possible that most K-selected strategies, like group territoriality, are inherently self-reinforcing, leading previously to the idea of orthogenesis (Southwood et al., 1974). The proposal that K-selection leads to increased intra-specific and decreased inter-specific competitiveness (Pianka, 1970; Southwood, 1976) allows us to predict that, in areas where G is similar, the proportion of species exhibiting group territorial behaviour should be related to the rate of immigration of r-selected species from elsewhere. This might explain the high proportion of group territorial species found in the relatively isolated Australian avifauna (Harrison, 1968; Rowley, 1976) and the relatively low proportion apparently occurring in tropical Asia (Zahavi, 1976), which is open to immigration on a broad front from the temperate Palaearctic region.

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The Selfish Behavior of Avian Altruists

Glen E. Woolfenden

Group-breeding birds provide excellent opportunities for studying the importance of altruism and selfishness in the evolution of sociality in animals. The Florida Scrub Jay *Aphelocoma c. coerulescens* is a group breeder in which many individuals do not breed, but instead participate in the breeding activities of others. Studies of a color-ringed population begun in 1969 at the Archbold Biological Station in south-central Florida, U.S.A., provide the data used for posing answers to two questions: Do helpers help the breeders? Do helpers help themselves?

General ecology

Before addressing these two questions, a brief overview of Florida Scrub Jay ecology is presented. The Florida population is a disjunct relict of a corvid species otherwise widely distributed in southwestern North America. Living only in the unique Florida scrub, Florida Scrub Jays are extremely habitat specific and extremely sedentary. They are long lived, with an adult annual survival that exceeds 80%, and both nearly permanently monogamous and permanently territorial. Normally single brooded, the population has a short, synchronized breeding season, March through June, and produces at most a few young per year. Where not persecuted, Florida Scrub Jays nearly ignore humans, which greatly facilitates field observation (Woolfenden, 1973).

Florida Scrub Jays normally do not breed until 2 or more years old, although they are capable of breeding at age 1 year. The pre-breeders tend to remain in their natal territories where they help the resident breeders care for their dependent young. Nesting success and survival of fledglings determines, in part, the number of helpers assisting a breeding pair. Only about half of the breeders have helpers during any given nesting season. Breeders with helpers average 1.8 per pair with a range of 1 to 6.

Do helpers help the breeders?

A variety of measurements have been used to test the hypothesis that Florida Scrub Jay helpers do increase reproduction for the breeders they assist. Unassisted breeders produce 1.3 fledglings per pair per breeding season (n=110); breeders with helpers produce 2.1 fledglings (n=124). The difference is significant. Unfortunately, several weaknesses exist when all breeders are included in the analyses. Novice breeders, which for certain other bird species are known to be less successful than experienced pairs (Lack, 1966), rarely have helpers, and therefore tend to fall in the category of unassisted breeders. In addition, it is logical to assume that breeders vary both in the quality of their genes and in the quality of their territories. In order to minimize these factors, reproductive success was measured only for pairs previously successful at fledging young. As the pairs were stable, they also tended to occupy the same space, their territory (Woolfenden & Fitzpatrick, 1978). The results parallel those obtained for the total sample. When the same, experienced, and

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spacially stable pairs lacked helpers, they produced fewer fledglings than when they had helpers (1.6 versus 2.6).

Starvation is virtually non-existent in the study population (WOOLFENDEN, 1978), therefore food provided for dependent young relative to food needed does not seem to influence reproductive parameters (e.g. clutch size and time of breeding). Forthermore, field observations show that virtually all nest failures result from nest predation. Loss of clutches prior to hatching was measured for breeders without helpers versus those with helpers, and the difference was significant: breeders with helpers hatch more eggs (WOOLFENDEN, 1978). The results were similar when only the experienced, spacially stable pairs were used in the analysis.

From these data and analyses it is concluded that Florida Scrub Jay helpers do help the breeders. It also is hypothesized that their help is related to nest predator dissuasion.

The question "Do the helpers help the breeders as individuals?" is an important subset of the previous question. By this I mean: do the helpers increase the longevity of the breeders? Survival of breeders between successive nesting seasons was found to be significantly different between pairs without helpers versus pairs with helpers (80% versus 87% per year) (STALLCUP & WOOLFENDEN, 1978). Therefore it is concluded that helpers help breeders as individuals as well as through increasing the frequency of their genes in future generations. Group defence against predators such as hawks (*Accipiter, Circus)* is the suspected way that helpers increase the longevity of breeders.

Before considering whether or not helpers help themselves, it is informative to know the genetic affiliations of the helpers to the breeders they assist. Table 1 lists the family affiliations of 139 helpers. Many of the 139 individuals helped for more than one season, thus the sample includes 199 seasonal breeding attempts. In 60% of the cases the helpers helped both their parents. These data provide the correlation that suggests kin selection as the major causative factor in the evolution of helping behavior.

TABLE 1: Whom helpers help – based on 139 known-age helpers during 199 seasonal breedings

breeders		helper seasons		
male	female	male	female	sex?
father	mother	52	53	13
father	stepmother	14	8	4
stepfather	mother	5	11	4
brother	unrelated	5	1	0
prob. brother	unrelated	3	0	1
half-brother	unrelated	3	0	0
unknown	unrelated	6	0	0
grandfather	mother	1	0	0
first cousin	mother	1	1	0
prob. uncle	grandmother	1	0	0
unrelated	unrelated	1	2	0
unknown	unknown	5	3	1
		97	79	23

Many additional interesting filial relationships between helpers and breeders are revealed by Table 1. For example, step-parents have relatively fewer helpers of like sex than of the opposite sex. We suspect this results from the need for breeders to dominate helpers of the same sex in order to prevent cuckoldry or loss of limited resources (Woolfenden & Fitzpatrick, 1977). Their attempts to dominate seem to result in the departure of some potential helpers. Another is that males help breeders that do not include either parent more often than do females (26 versus 7 in Table 1). In part this is accounted for by the fact that males help for more years than females. It also may be that males have more to gain from helping than do females.

Do helpers help themselves?

Helpers do increase the reproductive success of breeders, and the breeders they help usually are close relatives. Therefore clearly helpers are helping themselves indirectly by increasing their inclusive fitness. The question remains: do helpers help themselves as individuals?

The close observation of hundreds of helpers for 10 consecutive breeding seasons has yielded no suggestion that helpers contribute their gametes to the production of offspring. Thus they receive no direct reproductive benefits as helpers.

As mentioned earlier, breeders live longer when associated with the pre-breeding helpers. From this it seems logical to suspect that the pre-breeders live longer by associating with breeders. Unfortunately we have devised no test for this supposition. Florida Scrub Jays exist in one of three classes, dependent young, helpers, or breeders. Non-breeding non-helpers with which to test the supposition are virtually nonexistent. Characteristics of dispersal support the supposition, however, in that rarely do the jays depart from the presumed safety of their helping (usually natal) territory before having discovered a space for breeding. Thus Scrub Jay dispersal consists of forays into the surrounding territories and frequent return to their helping territories as opposed to permanent departure in order to seek breeding space.

Both males and females practise dispersal forays. Males have an additional means of obtaining breeding space. The sequence of events, outlined recently (Woolfenden & Fitzpatrick, 1978), is as follows: (1) Helpers increase the reproductive success of the breeders they assist. (2) As the family increases in size its territory also tends to increase in size. (3) Territorial growth often is followed by a process we term territorial budding, in which the dominant male helper comes to reside in a segment of the group territory, (4) where he pairs, always with a female from outside his group, and commences breeding.

Conclusions

In conclusion, it may be that Florida Scrub Jay helpers behave only in ways that maximize their success as breeders. If this is true, then increasing the representation of relatives in the population emerges as supportive rather than causative in the evolution of group breeding. Finally, we suggest that the need now is for investigators to identify and quantify the selfish benefits and to compare these with the more easily measured inclusive benefits of helping to raise kin.

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Breeding System and Strategies of Ostriches

Brian C. R. Bertram

Introduction

The aims of this paper are threefold. The first is to summarize information on the communal nesting system of the Masai Ostrich *Struthio camelus massaicus* in East Africa. The second is to examine the costs and benefits of the different reproductive strategies open to the different classes of individuals in the population. The third is to consider what factors contribute to the evolution of the communal nesting systems of Ostriches and Rheas *Rhea americana* (Bruning, 1974).

It is valuable to concentrate on the Ostrich breeding system at this moment for three reasons. First is because it is important to understand the operation of each species' system before it can be fitted into the more general picture of what ecological and social factors favour the evolution of co-operative breeding in birds in general. Second, the Ostrich system does not in fact fit into any of the usual categories of co-operative breeding in birds. And third, hearsay reports of the Ostrich breeding system are being printed in advance of any formal published account of the observations.

Summary of the Ostrich breeding system

The data on which this account is based have been collected entirely in East Africa, to a small extent in the Serengeti National Park in Tanzania, but mainly in Tsavo West National Park in Kenya. It should be borne in mind that this account refers to the Masai Ostrich only, and that this subspecies may differ in its breeding system from that of the South African Ostrich *S. c. australis* (Sauer & Sauer, 1966).

The observations in Tsavo were made during the Ostrich nesting season from July to October 1977, and are continuing. Birds were observed from a vehicle, using binoculars from distances of 30 m to 3 km. At least 25 birds could be recognized individually. 18 nests were found and observed. All eggs were weighed, measured, photographed, and individually marked.

The adult population density was of the order of 1 bird per 5 km^2. The adult sex ratio was biassed, with 1.44 females per male. They were often solitary (49% of sightings), or in groups of two birds (35%), three (9%), four (5%) or five birds (2%). These aggregations were loose, temporary, and of varying composition.

During the breeding season, each male remains within a poorly defined territory of about 14 km^2 in area on average. Females drift through the territories of at least three or four different males, who display to them frequently, and they mate promiscuously with different males.

One or more shallow scrapes are made somewhere within the territory, and eggs are laid in one of these. The first bird to lay in a nest scrape is the 'major' hen (after Sauer & Sauer, 1966); she is the bird who will later guard and incubate the nest. Other females –'minor' hens – also lay in the nest, in the early afternoons. Each female lays an egg on

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alternate days. The rate of appearance of eggs in the nest increases with time, as more females, up to four or five of them, lay in it.

In Tsavo, the nest is guarded from quite an early stage: when it has more than 5–10 eggs in it, there is usually a bird in attendance throughout. Guarding prevents destruction of the eggs by Egyptian Vultures *Neophron percnopterus,* and probably helps to prevent predation by hyaenas *Crocuta crocuta* and jackals *Canis mesomelas.* Nonetheless the predation rate on nests is high – probably well over 75 %. The major hen guards during the day, and the male at night; the minor hens play no part in nest guarding. Changeovers take place about two hours after sunrise and before sunset, allowing a major female only about four hours per day in which to feed. Mating often takes place at the time of the changeover.

The completed nests observed contained between 20 and 35 eggs, and even larger clutches have been reported. When incubation starts, many of the eggs are pushed out of the nest itself and into a surrounding ring 1–2m away, leaving 18–25 of them together in a central group. Only these central eggs are incubated. The eggs pushed to the outer ring remain permanently there; they do not start to develop, are exposed to the full sun, and are doomed. I do not yet know which individual arranges the eggs in this way.

Incubation, which takes about 6 weeks, is carried out by both the male and the major female, with a similar schedule as when guarding the nest. The pair both attend and guard the young. HURXTHAL (1973) described the process whereby pairs merge their chicks with others into large groups, and reported that chick mortality was high. In captivity, Ostriches are reported to come into breeding condition at 3 years old, and to live until at least 40 (SMIT, 1963).

The fitness of the different reproductive strategies

It is sufficient in the case of the Masai Ostrich to consider only the reproductive output of individual birds, rather than their inclusive fitness (HAMILTON, 1964), because the degree of relatedness among any two adult birds laying in the same nest must be both very low on average, and impossible for the birds to determine because of the promiscuity and mixing of eggs. The reproductive output of birds using each strategy will in principle be able to be quantified, when more data have been collected. At this stage, however, it is worth examining in more general terns the costs and benefits of the different strategies.

Male

The male's main option appears to be whether or not to start a nest. Most, and possibly all, do so. It is possible that owning a nest enables a male to obtain improved mating opportunities with minor females who may visit his territory in order of lay in it. Almost certainly he gains preferential mating access to the major female, who in addition is 'anchored' at the nest and therefore during those hours she is unable to mate with other males. The male, on the other hand, despite owning a nest, is still free to mate promiscuously with other females, because he is not obliged to be in attendance at the nest during most of the daylight hours.

Minor hen

The minor hen's main option is whether or not to lay in another bird's nest. With the biassed adult sex ratio, about a third of females have no mates, and it is unlikely that they

would be able to care for a nest alone. Therefore in order for these birds to reproduce at all, they clearly must lay in other birds' nests. Other minor hens are probably major hens elsewhere, with mates, and owning nests which have been destroyed and not yet re-started. A third category may be potential major hens who have not yet started their own nests.

Females appear to know of, and they occasionally visit, other nests in addition to the one in which they are laying, and therefore a minor hen has the secondary choice of what nest to lay in. Nests nearer completion will be vulnerable to predation for less long, and may by their survival so far have shown themselves to be in particularly good localities. On the other hand, nests with fewer eggs, especially if these have mostly been laid by the major hen there, may afford the minor hen's eggs a better chance of remaining among the incubated centre group. It should prove possible to quantify the consequences of each of these choices.

Major hen

The major hen has a wider range of options. Her first is whether to start a nest instead of laying in other birds' nests. The costs in predation and energetic terms are probably negligible. However her feeding opportunities are reduced, and possibly with this the number of further eggs she can lay. On the other hand, if these are already limited by other factors, starting her own nest gives her an additional place in which to lay, and one in which her eggs may receive favoured treatment (see below).

Another of the major hen's options might be to prevent the minor hens from laying in her nest. The male is unlikely to be nearby to assist her, and his genetic interest in doing so will be less than hers because he has mated with those minor hens. She makes no obvious attempt to prevent the deposition of extra eggs; it would be difficult for practical reasons for her to be successful at it without either neglecting the nest or by her activities rendering it conspicuous to predators such as lions *Panthera leo.*

It is probable that the major hen benefits from the presence of the extra eggs by a process of dilution: if a predator removes one egg, it is less likely to be one of her own. This protection by dilution (Bertram, 1978) can work (a) provided that nest predation does not always destroy the whole nest (it does not – 91% of surviving nests had one or more of their eggs destroyed), and (b) provided that larger nests are not proportionately more vulnerable than smaller nests (data on nest predation with increasing nest size are difficult to evaluate but do not indicate any appreciable increase at all).

It is only worthwhile for the major hen to protect her eggs by diluting them with others if she can incubate more eggs than she can lay herself. It is not clear whether or how she may be physiologically limited in her laying capacity. However, she may be limited by time. To lay all 20–25 central eggs would take her 40–50 days, and thus stretch by some three weeks the length of time during which nest destruction could take place. In addition, it is likely that the hatchability of the first-laid eggs would start to decline sharply over that length of time, possibly due in part to water loss (measured at 1.5–2 gm per day) as well as to the prolonged effects of high temperatures.

A fourth option open to the major hen is to arrange the eggs in the nest so as to favour her own. It should be noted that this option is also open to the male, that his best arrangement would be the same as hers, but that he would benefit less than she would by

any such arrangement. By recognizing common motherhood of different eggs (by dimensions, weight and pores) in one nest I was able to determine that none of the 9 eggs in the outer unsuccessful ring belonged to the major hen, whereas she was the mother of 9 of the 19 eggs remaining in the incubated central group. Further work is in progress to determine how general and how successful such discrimination is, who performs it, whether it depends on recognition of a bird's own eggs (or for example by location), and if so how this is achieved. Clearly any degree of successful discrimination improves the reproductive success (from that nest) of the major hen compared with the minor hens.

Factors contributing to the evolution of the Ostrich nesting system

Large size

At 1300–1900 gm, an Ostrich egg comprises only about 1.5% of adult body weight. This is in agreement with the general trend across bird species that the larger the bird the relatively smaller the egg it lays (LACK, 1968). It is not known what factors cause this trend, but among them may be problems of protein or calcium intake or mobilization. In general, the larger the egg, the proportionately greater is its shell weight – about 20% in the case of the Masai Ostrich. It is possibly because of the considerable thickness of the shell to be produced that the Ostrich hen is able to lay only small eggs and not more often than on alternate days. The small size of the eggs means that a bird can cover proportionately more of them, and the slowness in producing them means that it may not be worth her while to lay as many as she is capable of covering. It also means that it does not cost her a loss in fitness to incubate extra eggs of other birds.

Sex ratio

The bias towards females in the adult sex ratio means that there are many females who are without mates and are therefore compelled to be minor hens. It is not known what causes the unbalance in the sex ratio, but a slightly higher rate of predation on the more conspicuous males throughout the year could cause a considerable divergence in a long-lived species.

Predation

As with the skewed sex ratio, a high predation rate on nests during the laying stages means that there are many females with eggs to lay but with no nests of their own to put them into. As well as increasing the number of birds with spare eggs, and therefore the final clutch size, it also increases selection pressures to reduce the duration for which a nest is in existence (PERRINS, 1977). It increases the cost of not guarding the nest, and therefore may influence how many eggs major hens can lay, and whether one (as in Rheas) or two birds (as in Ostriches) are required to look after the nest.

Temperature

High temperatures probably accelerate the decrease in its hatchability as an egg gets older, and may thus limit the number of eggs which it is worth laying before incubation starts. Temperature influences the need to attend to the nest to shade the eggs, in the same way as to guard them against predators, and may thus similarly influence whether one or

two birds are necessary to look after a nest successfully. Temperature may influence the egg colour, which in turn probably influences their vulnerability to predators: the creamy white colour of Ostrich eggs probably prevents them from heating up as much as would a camouflaged egg, but it makes them much more conspicuous to aerial predators.

Food distribution and availability

These will clearly have an effect on the breeding system, in several ways. Among these are in determining the population density, in influencing the grouping and foraging behaviour of adult birds, in determining the extent to which birds can achieve their physiological and nutritional requirements for laying large numbers of eggs, and in influencing the time for which a bird needs to be off the nest to take in enough food to continue with laying or incubating.

Because these various factors are diverse and interact with one another, it will be a difficult as well as a fascinating task to amalgamate them to understand the evolution of the communal nesting system of the Ostrich; but the first steps are being takes.

Acknowledgements

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Bee-Eaters: An Alternative Route to Cooperative Breeding?

Stephen T. Emlen and Natalie J. Demong

Introduction

Most current models of the evolution of cooperative breeding stress two points: (1) the population saturation of suitable habitat, which severely limits the options for territory establishment and breeding by new birds, and (2) the close kin relationship between breeders and helpers (generally direct offspring from previous breeding attempts). Colonial breeders offer unique possibilities for the study of "altruism" since (1) breeding sites are usually available in excess, and (2) the presence of large numbers of interacting individuals offers opportunities for social contact and bonding outside the family- or kin-group.

Of the birds of the world, only a handful are both colonial and cooperative breeders. White-fronted Bee-eaters *Merops bullockoides* are such a species. These are common birds inhabiting the savannahs of east and southern Africa. They are social throughout the year and breed in dense colonies ranging from 20 to 150 nests. Each nest consists of a burrow dug 0.5 to 2 meters into the ground or into vertical cliffs along river banks or ravines. Our studies indicate that roughly 60 percent of the nests in Kenya are tended by helpers, and that from 20 to 50 percent of the adult population may be non-breeders in any given season. All members of a breeding group share in virtually all aspects of nesting, from constructing the chamber, to incubating the eggs and feeding the young.

We initiated studies of the social organization of *Merops bullockoides* during the spring of 1973. We returned to Africa and continued our studies during both the autumn of that year and the spring of 1975, and we recently initiated a more intensive, longitudinal study that has been in continuous operation since January of 1977. Our study area comprises roughly 80 square kilometers in the southern end of Lake Nakuru National Park, Kenya. Over 500 birds have been individually captured, sexed (by laparotomy) and marked (by leg ring and individually identifiable wing saflag). Behavioural observations are concentrated on approximately 150 "focal" birds, whose locations, social interactions, group membership and status, and breeding contributions are regularly recorded. These data are complemented by demographic information on survival (calculated from monthly census records), dispersal, and fecundity (obtained by monitoring the success of all breeding attempts).

In this short report we would like to focus attention on three aspects of the breeding biology of the White-fronted Bee-eater in Kenya: (1) the reproductive options available to individual birds; (2) the contribution of helpers to breeding success (do helpers really help?); and (3) the complexity of social bondings and the dynamic nature of group membership. Finally we comment on the interpretation of bee-eater behaviour in terms of "selfishness" versus "altruism", and "kinship" versus "reciprocity".

Since our studies are continuing, this paper should be viewed as an interim report.

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Quantitative details of results presented, as well as theoretical models and interpretations presented, are bound to change as new data become available in the years ahead.

Reproductive options available to individual bee-eaters

Many tropical insectivorous birds time their breeding to coincide with the rains. Bee-eaters, however, often initiate breeding during the tail end of the harsh dry season, apparently anticipating the rains. In this way the period of hatching and nestling growth may be timed to the early rains, which bring with them a flush in insect food availability. Such a strategy leads to high productivity in areas with predictable rainfall such as West Africa (Fry, 1972a; Dyer & Fry, 1979) and southern Africa (Emlen & Demong, unpublished data).

The White-fronted Bee-eater in Kenya is faced with a more unpredictable and, often, a more harsh environment than its southern or western counterpart. Although textbooks describe Kenya as having two rainy seasons, the long rains of March, April and May, and the short rains of October and November, the visitor is most impressed by the tremendous variability in both the timing and the amount of rain that falls during any given year. Equally astonishing is the spatial heterogeneity of rainfall – monthly values frequently differ significantly at locations only kilometers apart.

If *M. bullockoides* is adopting the general bee-eater strategy of anticipating the rains, many such "anticipations" are unsuccessful as the rains come late or fail to materialize altogether. Many reproductive attempts are unsuccessful and losses due to nestling starvation can be impressively high. Conversely, when rains are unusually heavy, rivers rise rapidly and can reach the point of covering the nesting holes and drowning the eggs and nestlings inside. The contents of two entire breeding colonies have been lost in this manner.

It is difficult to use the general terminology found in the literature on cooperative breeding and speak in terms of territory "saturation" or breeding "openings" since nest chambers are not a limiting resource and can be dug at any time. The highly variable and often harsh environment of the Rift Valley suggests there are very different levels of parental (or group) investment that might be needed to successfully rear young during different seasons. The assessment of these ecological conditions appears to be extremely important for an individual bird that is weighing the costs and benefits of the strategies of independent breeding versus remaining or joining a breeding group as a helper.

Figure 1 shows the average starting group size of breeding units in different colonies plotted as a function of the rainfall occurring during the month prior to egg laying. The positive relationship is consistent with the hypothesis that individual bee-eaters are assessing the ecological potential for successful breeding, and choosing to remain as helpers when conditions are harsh and the chances for successful reproduction low, but are opting to leave established units and initiate breeding independently when ecological conditions (here being estimated by rainfall alone) appear favourable.

We propose that the environmental instability and unpredictability in Kenya preclude the attainment of any steady state population whose density is at carrying capacity. The equivalent of breeding "openings" occur when conditions are favourable; they "close" when times are harsh. This model leads to the prediction that the incidence of helping

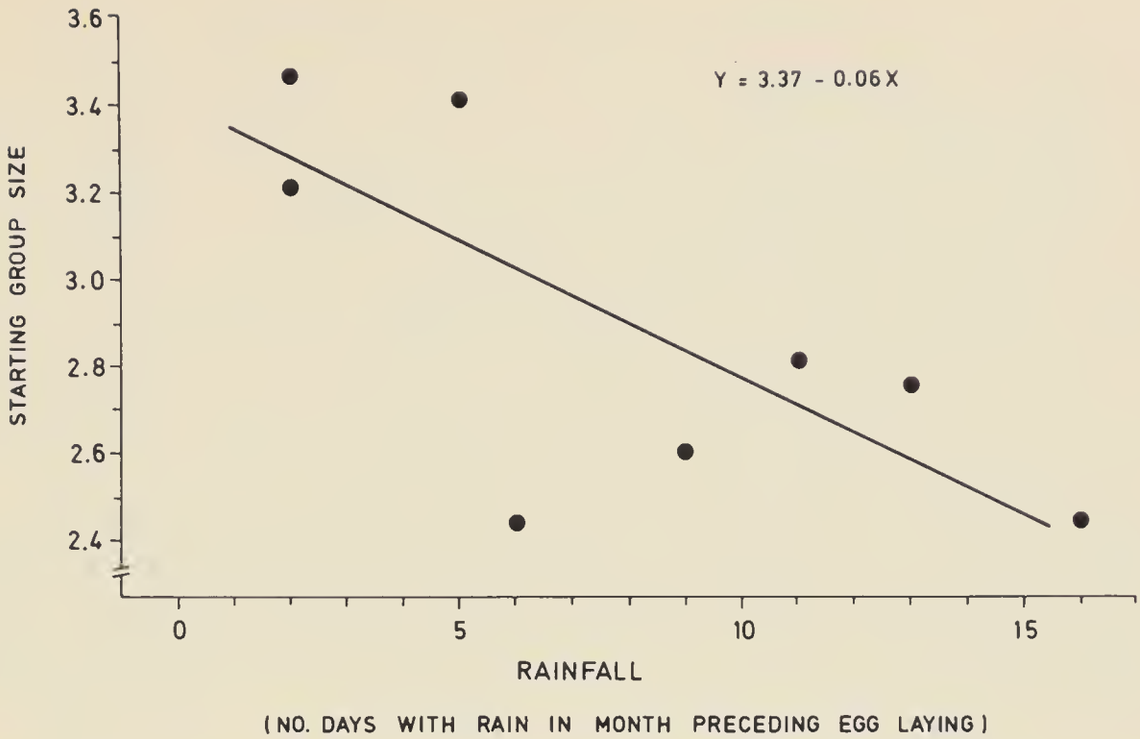
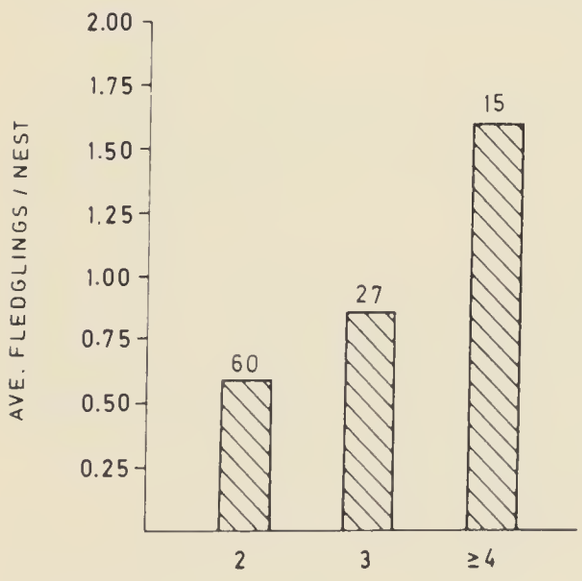


FIGURE 1. The relationship between average starting group size and rainfall in the month preceding egg laying. Each point represents the mean starting group size for a single breeding colony.

should be both greater and more variable in Kenya than in areas where the rainfall is more regular and predictable. This trend is borne out in comparisons of group size in our Nakuru study area with those of *M. bullockoides* in southern Africa (EMLEN & DEMONG, unpublished data) and *M. bulocki* in Nigeria (FRY, 1972a).



	PAIR	GROUP
SUCCESSFUL	22	28
UNSUCCESSFUL	38	19

$x^2 = 4.67$

$p < .030$

FIGURE 2. The relationship between nesting productivity and group size. The numbers at the top of each histogram represent the sample size (number of nests). In the lower contingency table, "successful" denotes the number of nests that reared at least one young to fledging age. (All data from colonies MBAA, MB, ESI, and AH from 1977 and MM1 and MM2 from 1978 are included.)

The contribution of helpers to breeding success

In the four years of our study, we have collected data on reproductive success at twelve different breeding colonies. The magnitude of any benefit accruing to a breeder through the actions of a helper can be measured by comparing the number of fledglings produced by pairs with similar productivity values from groups containing one or more helpers.

Environmental conditions and reproductive success in the different years were variable enough to preclude a pooling of all the data. Results from six breeding colonies nesting under similar conditions during the long rains of 1977 and 1978 are presented in Figure 2. Nests that were lost due to chance catastrophic effects (to safari ants or flooding, where group size could play no role in influencing success) have been omitted from analysis.

The mean number of fledglings produced per nest is histogrammed as a function of group size in Figure 2. It is apparent that helpers do play a significant role in increasing the successful production of young, with groups of four rearing over twice the number of young as pairs alone. Similar trends were apparent in the data from 1973 and 1975, but the magnitude of the differences, as well as the overall mean reproductive success, differed in the different seasons.

Social dynamics of bee-eater groups and the "sources" of helpers

A general finding in studies of cooperative breeders is that helpers generally are young from previous breeding attempts that remain with, and assist, the family unit. The social unit thus is relatively "closed" and helpers and breeders are close kin.

White-fronted Bee-eaters, by nesting colonially, daily come into contact with many individuals from outside the direct family unit. This raises the possibility that social bonds may be formed with a larger number of individuals, many of whom may not be close kin. It also presents opportunities for various subtle forms of behavioural competition, manipulation, and even cheating within and between the numerous "cooperative" units that coexist in the matrix of the larger colony.

By following individually marked birds over long periods of time, we are attempting to learn more about these questions. The picture that is emerging is one of great complexity, with bee-eater groups having a fluid and dynamic membership in which individuals regularly leave the group, visit or mix with other units, and frequently return in later months to roost or nest again with individuals with whom they have shared a prior common membership. Figure 3 shows an example of a "flow diagram" of the locations and group memberships of a small subsample of individuals as they shifted over a ten month period between two successive breeding attempts. Six specific individuals will be traced as illustrations of types of dynamic interactions that have been observed to date.

Individuals 116 and 46 were a breeding pair nesting in hole number 7 at MBAA colony. Shortly after their eggs hatched, the colony was flooded by high river waters. Both birds left the colony site, wandered 300 m downstream, and joined with two other individuals roosting in a new hole at this new sub-colony, MB. The male, 116, occasionally also roosted in a second chamber coinhabited by an additional male and female. Nine months after their original nesting failure, 116 and 46 initiated breeding in still a third location, hole 65 in a new colony, MM. During the non-breeding interim, each bird had mixed and

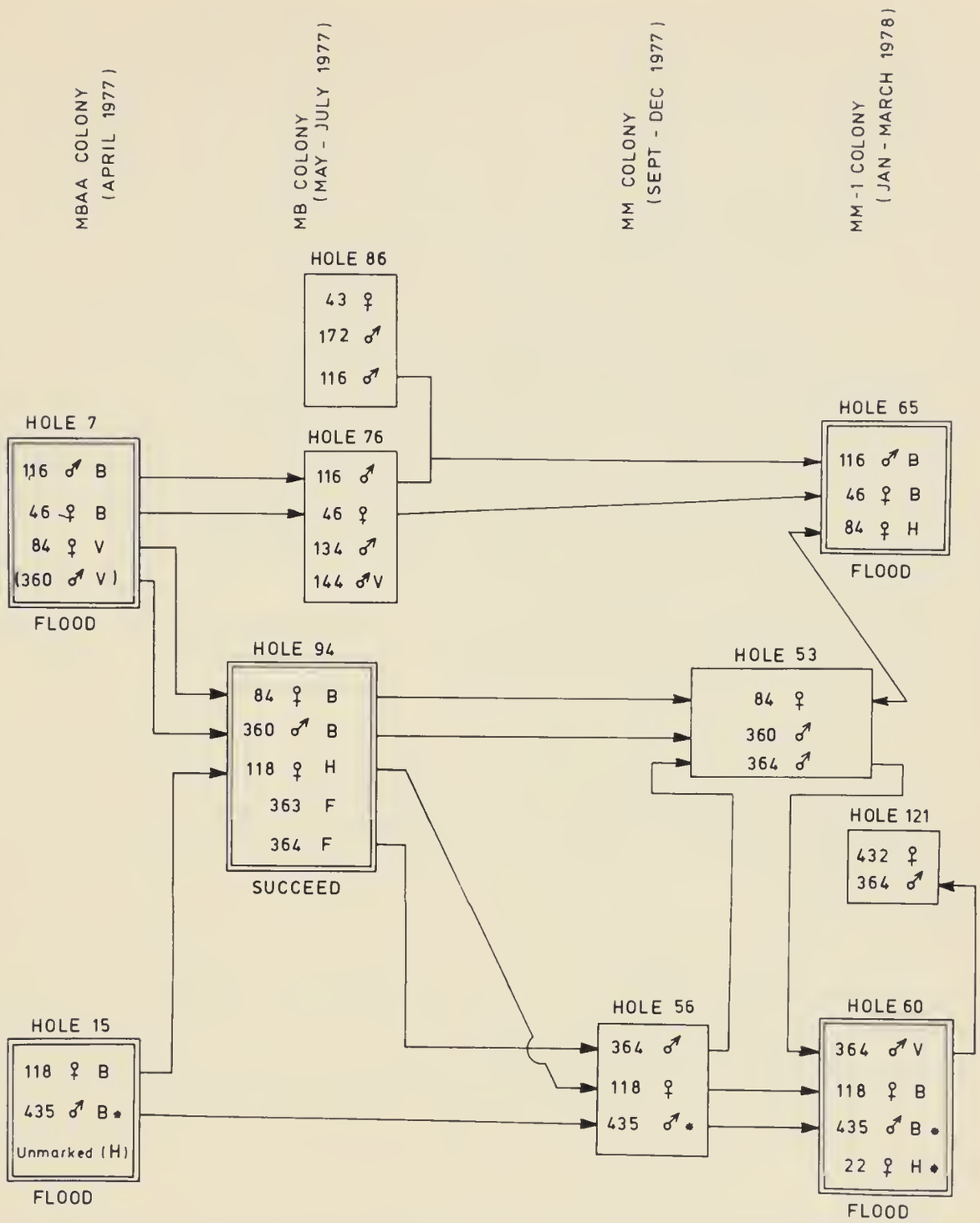


FIGURE 3. Flow diagram showing the mobility between social groups in the White-fronted Bee-eater. Each box represents a breeding (double outline) or roosting (single outline) chamber. The birds residing at that location are identified by band number, sex, and status. B denotes breeder; H denotes helper; V denotes visitor; and F denotes young fledged from that nest. Parentheses indicate presumed rather than confirmed status. An asterisk indentifies "yellow morph" individuals. For a detailed explanation of the fates of selected individuals, see text.

roosted with other individuals of both sexes; yet they showed mate fidelity when renesting in the following year.

Female 84 was first seen as an accepted visitor to 116 and 46 at MBAA. However, it did not join this group, but travelled the few hundred meters to the MB sub-colony, where, together with male 360, it bred in hole 94. They were joined later by a female helper and, together, successfully reared two offspring.

In the following few months, 360 and 84 moved again, this time to colony MM, approximately 2.5 km upstream. They roosted together, but failed to breed when the colony nested in January and February of 1978. When the rest of the colony hatched young, female 84 returned to visit and feed the young at hole 65. The breeders in this hole were 116 and 46, the same adults she had visited the previous year. A kinship hypothesis would predict that she was returning for a second year to help her genetic parents. But, in the interim, she had mated, bred, and successfully reared two offspring.

Another case history is provided by female 118, the presumed breeder in hole 15 at colony MBAA. Her nest also was destroyed by flood waters and at this time she left her original unit and joined hole 94 at colony MB where breeding was in progress. Thus her path and those of 360 and 84 converged at this point. Following the successful rearing of two fledglings, female 118 took up residence in hole 56 in the new colony MM. Her coinhabitants were male 435 (her previous mate before the flood some months earlier), and one of the young birds fledged from hole 94. This yearling (364) divided its time between its parental group (residing in hole 53) and its foster group (in hole 56). The foster group later shifted to a different hole in the MM colony where they were joined by another female helper and initiated breeding. Thus again members of a mated pair split, wandered, mixed with other individuals, and then regrouped showing fidelity for a later nesting attempt.

The potential contribution that would have been made by the yearling is unknown, since it split off and began roosting with a presumptive mate (a yearling female) in an independent hole shortly after the foster group initiated incubation. But its close social ties with 118 and 435, and its attendance at hole 60 raises the interesting suggestion that it might have been "recruited" from the unit in which female 118 had participated as a helper the previous season.

The last example is female 22. She is a rare "yellow throat" morph that comprises 0.5 percent of the population, and it was she who joined hole 60 at MM as the additional helper. The breeding male in that hole (435) was also a "yellow throat" morph. No additional information is available on the genetics underlying the yellow morph, or on the past relationships of these two individuals. But it again raises the possibility that kin may split for long intervening periods only to regroup in some later breeding attempt.

Much additional, longitudinal, data will be required before we have a full understanding of the kinships and reciprocal friendships that underlie what appears to be a very fluid and dynamic social system.

Selfishness versus altruism, and kinship versus reciprocity in the evolution of cooperative breeding in the White-fronted Bee-eater

Most sociobiologists are in agreement that kin selection is a logical and ever-present extension of individual selection. The key question concerns not the theoretical correctness of kin selection, but whether the kin component of selection is ever strong enough to counteract an individual component and lead to the evolution of social interactions or social systems that are not totally explainable in terms of individual selection alone. In the Red-throated Bee-eater of West Africa, Fry (1972a) believes that helpers sacrifice individual fitness and contribute to the greater production of offspring by their genetic

parents. In the White-fronted Bee-eater, although this model is tenable, the situation seems more complex. During the breeding season, the presence of helpers does contribute significantly to the fitness of breeders; further, helpers and breeders frequently (although perhaps not always) are kin. Thus their behaviour could be interpreted as "altruistic" or "cooperative" (sensu Hamilton, 1964).

On the other hand, the relationship between group size and favourable ecological conditions is consistent with the more "selfish" interpretation that each individual bee-eater assesses the costs and benefits of helping versus breeding and makes the decision that maximizes its own inclusive fitness.

Even when opting to be a helper, several potentially selfish gains might be realized (aside from the inclusive fitness gained if the helper assisted in rearing genetic kin). The social mobility of individual bee-eaters leads to the formation of social bonds that apparently are reciprocated, or at least reestablished, later in life. If our interpretation of the data in Figure 3 is correct, social bonds that formed while helping led to the potential recruitment of a helper for a future breeding attempt by female 118. And female 46 later reciprocated 360 and 84, joining their subsequent breeding attempt as a contributing helper (not shown in Figure 3). Thus helping may lead to the establishment of social bonds that provide selfish benefits to the helper during later breeding seasons. Helpers probably also gain valuable nesting experience, and benefit from the social acceptance and security that are afforded by group membership.

Thus the question of selfishness, reciprocity, and cooperative kinship remain unresolved at this stage of our study of the breeding biology of the White-fronted Bee-eater.

An individual bee-eater is not locked into a specific strategy of either breeding or helping for the entirety of its lifetime. Individuals have already been followed as they have shifted from helper to breeder to helper and vice versa. It seems most logical to approach this question of helping by considering the options available to a bird for independent breeding, and to weigh these against the costs and benefits of helping. As social and ecological conditions change, so will these options, their costs and their benefits. The highly variable environment of Kenya should thus prove to be a fertile testing ground for theories on the adaptive significance of cooperative breeding.

Acknowledgements

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SYMPOSIUM ON
THE SCIENTIFIC BASIS OF CONSERVATION

7. VI. 1978

CONVENERS: V. M. GALUSHIN AND J. J. HICKEY
CHAIRMAN: KAREL VOOUS

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Cooch, F. G. & H. Boyd: Waterfowl Conservation in North America 912
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Ecological Basis of Extinction in Birds

Warren B. King

Since the upper Jurassic when *Archaeopteryx* made its last glide to the earth's surface to become immortalized between layers of lithographic limestone in Bavaria, many thousands of species of birds have evolved and most of them have become extinct. Brodkorb (1960) estimates that through geologic time 1.6 million bird species have existed. We are left with about 9 000 species, the result of compromises between evolutionary processes and processes of extinction. Changing conditions of geography and climate trigger the processes that result in genetic isolation of populations and impose environmental stress to which these isolated populations either respond successfully, to carry on their lineage, perhaps altered somewhat in phenotype and genotype, or they succumb, unable to cope with the strain of surviving in a changed world.

Wetmore (1951) states that the class Aves reached its maximum abundance in the Tertiary, and that the species and genera we are left with today had their origins not earlier than the Miocene and Pliocene periods. The maximum number of species of birds extant at any one time has been suggested to be about 12 500, but the maximum expected longevity of any bird species is likely not to have exceeded 1 million years.

The four major glaciations of the Pleistocene imposed serious strains on many plants and animals. Brodkorb (1960) has estimated that up to 25 percent of the Pleistocene avifauna met extinction, so that we may reckon with about 12 000 species of birds toward the beginning of that epoch, but roughly 9 000 at the end. He estimates the average longevity of Pleistocene avian species to have been about 0.5 million years, but during the latter two glaciations this figure was reduced to 68 – 90 000 years. Fisher (1964) determined that the average longevity of species at the end of the Pleistocene was about 40 000 years, and since 1680, the year before the extinction of the Dodo *Raphus cucullatus*, the average longevity of a bird species was further reduced to 16 000 years. Thus, the expected rate of extinction has increased from one extinction every 83.3 years in the early Pleistocene to one extinction every 3.6 years in recent times.

While man cannot have had any role whatever in the extinction of 99 percent of avian species, there is evidence for human agancy in almost every extinction since the late Pleistocene. Martin (1967) includes moas (Dinornithiformes) of New Zealand and elephantbirds (Aepyornithiformes) from Madagascar in his case for direct human agency as the causative factor behind "prehistoric overkill," the puzzling disappearance of a substantial number of genera of large homeotherms following the retreat of the most recent glaciation, without replacement by competitors, and coincident with the spread and build-up of human hunting cultures. Moa and elephantbird remains have been found in quantity in human middens. There is no question they were hunted, presumably both for food and for raw materials for man's material culture. Undoubtedly they were hunted selectively over smaller game also. The quantities of recent fossil material of these enormous birds – the remains of 800 birds have been found in one 170–m^3 pit (Duff, 1952)

International Council for Bird Preservation, Smithsonian Institution, Washington, D. C., USA.

– can be explained not only by the fact that larger, heavier bones preserve more readily through time than thinner, more delicate ones, but also that generations of hunters concentrated the skeletal remains of these birds at a limited number of sites. If one assumes that hunting man had a hand in causing the extinction of a number of genera of large continental mammals as well, perhaps the reason only one genus of large Pleistocene mammal out of 14 that became extinct on the North American continent following the Wisconsin glaciation has been definitely associated with human artifacts (JELINEK, 1967) was that most were too large to move to a site of human habitation so that they had to be processed in situ.

A major consideration in trying to determine if the moas and elephantbirds became extinct from "natural" causes or at the hand of man is that both groups occurred on islands, very large islands to be sure, but with limited areas of suitable habitat supporting countable numbers of large birds. The repeated use of fire, as suggested by charcoal horizons in the soil on South Island, New Zealand (DUFF, 1963), is one likely way hunters controlled and restricted movement of moas to make them more accessible.

The preponderance of island forms in the list of avian extinctions since 1600 is striking. In an updated list of 92 species and 83 subspecies of birds extinct since 1600 (KING, in press), 93 percent were from islands. Avian extinction on continents has been very much the exception rather than the rule since 1600. Only 11 continental species and two subspecies have become extinct. The causes of extinction of continental birds have, with several exceptions, been the result of excessive hunting or habitat destruction.

Two of the eleven species, a sandpiper *Calidris cooperi* and a bunting *Spiza townsendi*, are known only from unique type specimens both collected in 1833 in New York state, United States. Both have been considered to be hybrids or sports although in neither case can the characteristics of the specimens be accounted for by hybridization or individual variation. No satisfactory explanation has been offered on these specimens. Three of the remaining continental extinct species and one subspecies were ducks *(Tadorna cristata, Camptorhynchus labradorum, Rhodonessa caryophyllacea* and *Anas georgica niceforoi)*. The last named, South America's only extinct bird in historic times now that the Whitewinged Guan *Penelope albipennis* has been rediscovered, was recorded as recently as 1952 and unconfirmed reports of *Rhodonessa* continue to the present. Hunting has been implicated as contributing to the extinction of all these ducks, but some other factor, as yet unexplained but likely related to destruction of some essential element of these species' habitats, may have been more significant than hunting in causing their extinction. It must be borne in mind that causes of extinction are in most cases presumptive. In most cases several causes have combined to depress replacement rates below mortality rates long enough to cause extinction. This cumulative effect is apparent today in many critically endangered species, for example many of the Drepanididae from Hawaii. Hunting is believed to have been at least a contributing cause of extinction in all other extinct continental forms with the exception of the icterid *Cassidix palustris* of Mexico, the courser *Cursorius bitorquatus* of India, and the babbler *Moupinia altirostris altirostris* of southern Burma, which were prohably most seriously affected by habitat destruction. It is worth noting that no continental bird species is known to have succumbed in recent times from predation, competition, parasitism, disease, genetic swamping or severe weather conditions.

Table 1: Presumed causes of extinction of birds on islands

Ocean	hunting	predation	competition	disease	genetic swamping	weather	habitat destruction	unknown
Indian	7	0	0	0	0	0	1	13
Atlantic	13	16	0	0	0	1	5	4
Pacific	20	96	18	15	2	0	46	11
	40	112	18	15	2	1	52	28

The causes of extinction of birds on islands have differed dramatically from those of continents. On islands the most important cause of extinction has been predation by mammals introduced intentionally or inadvertently by man (Table 1). Predation has been implicated as a cause in 70 percent of extinctions of birds on islands. Of these 54 percent are attributed to rats, among which the black or roof rat *Rattus rattus* is the most serious predator, although the Norway rat *R. norvegicus* and the Polynesian rat *R. exulans* are believed also to have made contributions. Documentation of rat predation is weak or nonexistent in most cases, although studies have documented rat predation of seabirds usually no larger than the rats themselves but in some instances as large as albatrosses (Kepler, 1967; Imber, 1975). Cats are implicated in 26 percent of extinctions by predation while dogs, mongoose *Herpestes auropunctatus*, the mustelids *Mustela nivalis* and *M. erminea*, pigs *Sus scrofa* and monkeys *Cercopithecus aethiops* have been implicated once or several times each. Among introduced avian predators, the owl *Bubo virginianus* has been suggested as a contributing cause of extinction of the Red-moustached Fruit Dove *Ptilinopus mercierii tristrami* of Hiva Oa, Marquesas Islands, in the 1920s (Thibault, MS.). The nominate form from Nuku Hiva was last recorded in 1849. Predation is not known to have caused the extinction of any of the 21 extinct birds of Indian Ocean islands. However, more than half of these were lost before 1800, long before careful records of such things were kept, so that it is likely that man's predaceous companions were at work there as well. An essential character of island species, setting them apart from continental species in terms of extinction processes, is a high susceptibility to predation as the result of evolution in the absence of predation.

Following predation, habitat deterioration or destruction is the most serious cause of extinction of island forms. Habitat destruction has been implicated as a cause of extinction of all 21 extinct Hawaiian passerines, and of all 10 endemic species or subspecies of Cebu Island, Philippines. In the latter case the situation is obvious: all the forest on Cebu was cut, and since all the endemic birds were adapted to forest, they all perished.

There has been conspicuous deterioration of the forests of the Hawaiian Islands since Captain Cook's visit in 1778. Cook and fellow explorers George Vancouver and James Colnett brought gifts to the Polynesian inhabitants which included goats, sheep, cattle, and probably black rats, measles and syphilis. Hawaiian King Kamehameha gave the grazing animals protection, and they flourished at the expense of the native vegetation, which had evolved free of thorns or chemical repellants in the absence of large herbivores. The effect of overgrazing of grasslands and forest is subtle in some areas, where elimination

of a few of the most highly palatable plants may be the only clearly discernible effect, and readily apparent in others, where erosion has left tiny islands of soil secured by unpalatable vegetation, standing a meter or more above bare rock. Exclosure of these animals by fencing at Hawaii Volcanoes National Park resulted in the immediate appearance of plants suppressed for generations, including the leguminous vine *Canavalia kauensis* Lamoureux 1972, previously undescribed but now abundant in the exclosure.

In spite of the effects of grazing animals, the precise cause of extinction of 21 Hawaiian passerines and the endangerment of 19 more is not yet clearly understood. One fable that should be put to rest is that the Polynesians lived in harmony with their land in Hawaii prior to Cook's voyage. The Polynesian population of the Hawaiian Islands in 1778 was 250 000–400 000. One century later following introduction of European childhood and social diseases, against which the Polynesians had no resistance, the population had declined below 50 000, and it is presently about one million. The impact of intensive subsistence culture on the lowland forests of Hawaii, particularly the dry lowland forests, must have been enormous. Pigs were introduced by the Polynesians and quickly spread to all corners of Hawaii's forests. Pig rooting is a conspicuous feature of Hawaii's forests even today. Dryland plants now comprise the bulk of the endangered plants of Hawaii, and only tiny fragments remain of dry lowland forest. Native passerines are virtually absent from the lowlands. On other tropical islands, for example Puerto Rica (Kepler & Kepler, 1970) the greatest avian species diversity occurs in dry lowland forest. Where then are the birds of the dry lowland forests of Hawaii? Discovery of skeletal remains of a substantial number of birds, including passerines and nonpasserines, some of which were flightless (Olson, pers. comm.), suggests that they may have been present when Polynesians first arrived in Hawaii over 1200 years ago. Bones of a flightless ibis have been dated at 25 000 years before present, and those of a flightless goose were prohably more recent (Olson & Wetmore, 1976). Both seem certain to have served as food for the early Polynesians. The destruction of lowland habitats by Polynesian Hawaiians started the most intensive wave of avian extinctions to have hit any part of the earth in the last millenium. The wave continues, for two species from Kauai, the honeycreeper *Hemignathus procerus* and the meliphagid *Moho braccatus,* the latter the last of five meliphagids from the Hawaiian Islands, are either extinct or so close that it makes little difference except to historians, while several others are not far behind.

Hunting has been a factor in 25 percent of extinctions on islands since 1600. Hunting was a significant cause of extinction in the 18th and 19th centuries (70 percent of hunting extinctions on islands occurred in these centuries), but in the 20th century hunting has ceased to be a factor due to widespread legal protection of birds or control of their harvest. Many of the species most velnerable to hunting disappeared early. Such well-known examples as the Dodo and solitaires (Raphidae) of the Mascarenes, the Great Auk *Pinguinus impennis* of the North Atlantic and the Spectacled Cormorant *Phalacrocorax perspicillatus* of the North Pacific, all flightless or nearly so, come to mind. These might be relatively common today had they survived to enjoy legal protection.

The most recent extinction of an island bird by hunting was that of the Wake Island Rail *Rallus wakensis,* which was apparently caught and eaten to the last individual by Japanese troops stationed on Wake in 1945. This is the only bird known to have been lost as the result of military exigencies.

Since 1600 the family Psittacidae has suffered more losses than any other family, 24 extinctions, plus several additional ones if one accepts as valid some of the Antillean and Mascarene parrots known only from questionable verbal descriptions. Hunting was a probable cause of extinction in all but five of these, although six others were lost so early that reliable information on causes of extinction is lacking.

Competition may have played a role in extinction of 18 birds, all from the Pacific. In all but two cases these were Hawaiian passerines which are thought to have been threatened by competition from species intentionally introduced to Hawaii to repopulate the lowlands with birds. Many of these introductions proved to be benign, but several, including the babbler *Garrulax canorus* and the white-eye *Zosterops japonica*, have invaded the last relatively unspoiled bastions of the montane rainforests where remnant populations of the rarer native Hawaiian birds persist. These introduced birds have not yet been shown conclusively to have affected the distribution or abundance of the native birds, so that competition as a cause of extinction in Hawaiian birds is based on surmise only. A more convincing case for competition as an agent of extinction is the disappearance of the race of the Grey Teal *Anas gibberifrons remissa* from Rennell Island, in the Solomons. This teal was restricted to a large freshwater lake, where it was hunted regularly but apparently not excessively. It disappeared in 1959, two years after the lake was stocked with *Tilapia*. Diamond (no date) suggests that effects of *Tilapia* on the lake's ecology were responsible for the teal's extinction, probably through competition for food.

Disease may also have been a factor in the wholesale extinction or endangerment of Hawaiian passerines. Native Hawaiian birds apparently have the same susceptibility to continental avian diseases, including malaria and pox, that the Polynesians had to the diseases of western civilization. Native birds taken to the lowlands within the altitudinal range of the introduced mosquito *Culex pipiens fatigans*, a malaria vector, quickly succumbed to mosquito-borne avian malaria (Warner, 1968), and native birds from above the altitudinal range of the introduced mosquito have shown no build-up of malaria titers in blood samples, whereas introduced birds carry uniformly low, but positive, titers. These relationships will be further clarified in the next few years by an intensive program of research on avian desease in Hawaii.

The extinction of the bullfinch *Loxigilla portoricensis grandis* on St. Kitts in the Lesser Antilles, last recorded in 1880, has traditionally been attributed to predation by green monkeys *Cercopithecus*. However, recent reassessment of the situation suggests that monkeys were probably not responsible for this extinction. Monkeys are not common in the high mountain forest where this bullfinch occurred. The bullfinch and a lower elevation congener *Loxigilla noctis* apparently lived in relative harmony with the monkeys for 200 years, but the high montane bird disappeared suddenly, it is postulated, as the result of two major hurricanes in 1899 (Raffaele, 1977). This is the only convincing case of extinction through natural causes in recent times.

An introduced monkey *Macaca irus* will shortly be responsible for the extinction in the wild of the pigeon *Nesoenas meyeri* and the parakeet *Psittacula echo* of Mauritius, however. Habitat destruction reduced the range of these species to a 1000-ha. area of forest, which supports a high monkey population as well. Monkey predation of nest contents has almost nullified reproduction for several years and neither species numbers more than 40 birds in the wild. The pigeon is now breeding regularly in captivity, where it

should persist as the first avian Père David's Deer. The kestrel *Falco punctatus* was also affected by monkey predation, but the last remaining breeding pair selected a predator-free nest site in a cliff pothole in 1975 rather than a customary tree site which was invariably predated. This fortuitous change in nest-site selection has been retained in the species, for in 1977 three pairs nested in cliff potholes, raising seven young.

No birds have become extinct as the result of parasitism, but two species, the wood warbler *Dendroica kirtlandii* of North America and the icterid *Agelaius xanthomus* of Puerto Rico, are endangered by selective brood parasitism by the cowbirds *Molothrus ater* and *M. bonariensis* respectively, both of which have recently undergone major range extensions which have permitted them to parasitize species that have not evolved defences against parasitism.

No species have been lost through hybridization, but two island subspecies have been lost as the possible result of genetic swamping by other forms of the same species. These include the owl *Ninox novaeseelandiae albaria* from Lord Howe Island, presumably swamped by repeated introductions of a mainland Australian subspecies *N. n. boobook* to Lord Howe, and the warbler *Cettia diphone restrictus*, of the Daito group south of Japan, presumably swamped by *C. d. riukiuensis* shortly after the type was collected in 1922. Several other birds are presently threatened by swamping. These include the grebe *Tachybaptus rufolavatus* of Madagascar which hybridizes frequently with *T. ruficollis* and which will soon be represented only by its genetic component in a hybrid swarm, the dove *Streptopelia picturata rostrata* of the Seychelles, whose phenotype has been replaced throughout its range by that of the introduced nominate race from Madagascar, and the partridge *Perdix perdix italica* of Italy, which has been swamped repeatedly by other subspecies introduced throughout Italy from game farms (Lovari, 1975).

Table 2: Chronology of extinction of birds on islands
Date of extinction

Ocean	1601–1650	1651–1700	1701–1750	1751–1800	1801–1850	1851–1900	1901–1950	1951–present
Indian	2	2	4	4	4	5	0	0
Atlantic	0	1	1	4	0	12	9	0
Pacific	2	1	0	8	12	36	45	9
	4	4	5	16	16	53	54	9

The rate of extinction since 1600 has varied considerably through time, reaching a peak around 1900 (Table 2). There has been no avian extinction in the Indian Ocean in the 20th Century. In the Atlantic Ocean the extinction rate peaked in the latter half of the 19th Century; in the Pacific Ocean in the early 20th Century. The primary causes have been predation, habitat disturbance, and hunting. Thus far in recent times extinction on continental areas has been remarkably light. However, comparison of the 1966 edition of rhe Red Data Book (Vincent, 1966) with the 1978 edition (King, 1978), currently in press, reveals the direction that extinction will take in the next two decades. We will continue to lose species on islands but at an increasingly slow rate. Those most vulnerable to man-induced changes on islands have already succumbed. The most significant change

on the earth's surface in the last two decades of importance to bird survival has been the accelerating rate of cutting of primary tropical forests of South and Central America, Southeast Asia, and Africa. In South America, for example, 15 taxa were listed as threatened in 1966: 79 are listed in 1978. Similar but less dramatic figures apply to the other areas of tropical continental forest.

One major difference between extinction rates of the future two decades and those of the past three centuries is that extinction-causing processes are now at work on the areas of the earth's surface with maximum bird species diversity, whereas formerly they affected mostly areas with depauperate avifaunas. As forests are destroyed in areas of high avian endemism, we can expect additions of tens of species to the list of extinct birds. For example the coastal forest of southeastern Brazil harbors 94 endemic bird species, and a slightly larger area including adjacent portions of Argentina, Paraguay, und Uruguay contains 196 endemic species (Ridgely, pers. comm.). In southeastern Brazil only three major tracts of primary forest, totalling 50 000 ha., remain intact. The remaining millions of hectares formerly covered with well developed primary forest are either clearcut or broken up into a mosaic of small stands, which may or may not be large enough to maintain any species over the long term. Similar circumstances now apply to portions of northern Colombia, and will apply increasingly to other continental areas formerly blanketed by tropical forest. It appears inevitable that the rate of avian extinction will increase well beyound one species per year by the year 2000.

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Waterfowl Conservation in North America

F.G. Cooch and H. Boyd

Waterfowl conservation in North America is a large and growing business. Although complete statistics are not available for Mexico, we know that in 1976, the latest year for which full details have been released, there were 2.5 million licensed sport hunters in the United States and Canada who killed and retrieved some 20 million ducks, 2.5 million geese, 10 000 cranes, 16 million woodcocks and 40–50 million doves and pigeons. The number of people who enjoyed seeing waterfowl were very much greater than 2.5 million, but their activities were less obvious and generally less demanding. Our purposes in this brief review are: to demonstrate the gains for bird conservation in general that result from the massive demands of waterfowl hunters in North America and the attempts by government to respond to those demands; to discuss some of the effects of man-made changes in the landscape on waterfowl populations; to look at some of the ways in which public expectations are changing; and, finally, to suggest how "waterfowl management" in North America is likely to be modified during the next 10 or 20 years.

It is generally assumed by the government officials responsible for waterfowl conservation that the supply of waterfowl must be shrinking, as the quantity and quality of wetlands are reduced by drainage and filling-in for agriculture, industry or housing. Habitat preservation is seen as the fundamental requirement. A basic belief of government managers is that severe restriction of hunting effort, by the use of short hunting seasons and small daily bag limits, is necessary to prevent excessive killing and to distribute kill fairly amongst hunters. These over-simplified beliefs do not necessarily correspond at all closely to the facts, but they are the basis for activities on a very large scale.

The laws of Canada and the United States are different in many important respects, but in both countries migratory birds, as defined in the U.S.-Canada Migratory Birds Convention of 1916, are the legal responsibility of the respective federal governments. They are not the property of individual landowners, at least while the birds are alive, nor of other levels of government (states, provinces, municipalities). However, landholders, industry and all levels of government must cooperate and contribute in order to maintain waterfowl populations at the high levels necessary to yield an annual 'harvest' (to use the common but misleading term for 'kill') of well over 20 million ducks and geese. Cooperate and contribute they certainly do: annual expenditures on migratory game bird research, habitat protection and management in North America exceed $ 300 million, with substantial amounts from special taxes, licence fees, and private donations but the bulk derived from general tax revenues. At least 30 000 biologists, land managers, law enforcement officers and support staff are actively engaged in some aspect of the management of migratory waterfowl in the United States and Canada. In addition, hundreds of thousands of volunteers give time and money to the wildlife conservation ethic. For example, in 1976 alone some 65 000 volunteers taught 700 000 young sportsmen the elements of hunter safety. Ducks Unlimited, a private organization, raised about $ 12 million, mostly in the U.S., to spend on wetland habitat preservation and improvement,

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mostly in Canada. By 1976, land acquired or set aside by governmental action (at all levels) in North America to provide waterfowl staging, breeding or wintering areas approached 200 000 000 ha, not including national or provincial or state parks. This represents a capital investment with a book value of much more than a billion dollars. In addition to lands acquired by governments, large tracts, often of the best wintering and staging habitat, have been preserved by private foundations and hunting clubs, generally to provide a place for their members to hunt.

Ducks are largely produced on or near lands of high agricultural value, whereas most geese breed in sparsely inhabited boreal and tundra regions. Most populations of geese, except for Atlantic coast populations of *Branta bernicla,* some subpopulations of *Anser albifrons* and Wrangel Island *Anser caerulescens,* are at or close to their highest recorded levels. Populations of ducks are being maintained at very high levels. There are substantial additional costs, many of them not widely recognised, in maintaining these population levels. For example, on the Canadian prairies serious damage to cereal grains occurs in years when harvesting conditions are wet and cut crops lie for a long time in swath, as the result of depredations by several million Pintails *Anas acuta* and Mallards *A. platyrhynchos.* On some large refuges, which may hold up to 300 000 *Branta canadensis* for several weeks or months, extensive feeding programs are required to discourage the dispersal of the birds, which would put them at high risk of being shot and perhaps increase depredation losses to farm crops. Such massive concentrations of waterfowl are inherently dangerous in terms of disease, stress, and breakdown of pair bonds, yet the alternatives may be worse.

A vast, almost self-contained bureaucracy has been assembled to regulate the kill, as well as to manage waterfowl refuges with a combined land and water area equal in size to Switzerland and East Germany (DDR) combined. The annual consultations of provincial, state, and federal agencies preceding the setting of hunting regulations (in May in Canada, in early August in the U.S.A.) bring together results from a vast infrastructure involving banding analysis, kill surveys, species-composition surveys, midwinter inventories, breeding-ground surveys with 100 000 km of transects, long-range weather forecasts, satellite imagery, and recommendations on harvest quotas. Few of the results of these endeavours are published in the scientific literature, although multilithed summaries are made available to other professionals in attendance at the meetings. The lack of thorough analysis, synthesis, and critical evaluation has led to an incredible duplication of effort, the perpetuation of redundant activities and abnormally slow improvement in understanding of the characteristics of the biological systems involved, so that the craft of waterfowl management is still in a remarkably primitive state. There are some notable exceptions, but the amount and quality of publications is not commensurate with the money, facilities and manpower available. It is estimated that the ratio of unpublished reports to published papers is 300 to 1.

There are 62 political units of North America for which hunting regulations have to be set. Management at the subpopulation level is attempted for some kinds of geese and the principal game ducks, with allocation of birds between hunters in different political areas. Population goals, usually expressed as a target number of breeding birds or the number to be left in late winter after the end of hunting, are gradually being established.

Detailed documentation of the distribution of many populations has been completed. Biologists can spend much of their working lives dealing with the Tennessee Valley

Population of Canada Geese, or the Mallard wintering in the High Plains of Colorado or the Canvasbacks *Aythya valisineria* of Chesapeake Bay.

To assure adherence to the waterfowl hunting regulations, not fewer than 3 000 full-time special enforcement officers are employed. The isolation of this group of applied ornithologists is nearly complete: they have their own land, agriculture, aircraft, journals, boats, police force, industrial base, legal advisors, laws, treaties – and their constituency of 2.5 million licensed hunters.

Although the Migratory Bird Convention of 1916 placed all migratory birds, not just waterfowl and other migratory game birds, under Federal control, migratory nongame species have until recently been largely ignored. It was judged that their continued existence was largely secure as they were not being hunted. As a result, the great majority of species falling under the aegis of the Convention were left to look after themselves. Scientists working on those species could not expect to obtain migratory bird management funds, the use of which was often restricted by law. Few Federal, Provincial of State biologists were involved in research on nongame birds and even fewer administrators.

The federal agencies became identified by ornithologists as nonornithologists and apologists of hunting; in turn, nongame-bird ornithologists were viewed by several generations of official game-bird managers as dabblers with no understanding of the real world, best suited to addressing garden clubs, shooting "song birds", and getting pleasure from seeing bird skins lying row upon row, all neatly labelled and reeking of preservative.

Wildlife conservationists and ornithologists rarely met, they belonged to different societies, read different journals, attended separate meetings, and generally viewed one another with suspicion. While legal authority for the protection of birds rested with the federal agencies, most of the contacts with those agencies enjoyed by the staffs of university departments and museums and by amateur ornithologists were only with their enforcement officers who regulate the issuance of scientific collecting and capture permits. Even the centralized bird-ringing offices with their 35 000 000 computerized records of banded birds and 3.5 million recoveries were largely concerned with game birds, and elaborate systems were developed to store, retrieve, and analyse recovery data by employing systems primarily of use to "managers".

Yet the truth is that both groups need each other and need to draw on each others' expertise, knowledge, and desire to protect essential habitat and, above all, the birds themselves.

A first tentative break in the allopatry came as a result of the widespread concern that followed publication of Rachel Carson's "Silent Spring". The Federal Authorities came to recognize that the quality of the environment was indeed vital to the well-being of all birds. Their response to this enlargement of their perception and, more importantly, to the increased expectations of the public was largely accomplished not by retreading wildlife ornithologists but by creating new "nongame" divisions, or by contracting out research.

Legislative and financial power was, and is, still vested largely in the hands of the hunters. Some programs of rehabilitation of rare and endangered species are being temporarily frustrated because any increase in the numbers of an officially designated rare and endangered species that results in its spreading into areas where hunting of abundant game species is important may lead to serious conflicts – for example, the closing of hunting in three counties of California because of the presence of Aleutian Canada Geese,

or the closing of a hunting season for Sandhill Cranes in Saskatchewan, because of the presence of a single nonbreeding Whooping Crane somewhere in an area of 100 000 km^2.

Yet many rare and endangered or threatened species of birds in North America owe their continued existence to the very large areas of protected habitat acquired to maintain populations of migratory game birds. In recent years habitat-management programs initially designed to enhance the usefulness of an area to game birds have often been modified to protect habitat essential to the maintenance of numerically rare species. It came as somewhat of a surprise that 53 birds and mammals listed by the U.S. and Canada as being rare and endangered, survived on lands acquired to protect migratory game birds.

There are other gradual shifts in emphasis being exhibited by the game-oriented public-service agencies toward the needs of nongame birds. Progress is not as rapid or massive as we would desire: not because the birds are not important, but because there is not a clearly identified, licensed, revenue-producing public, interested in birds per se. Even the most ardent game-bird ornithologists will agree that more people spend more money and more time watching, feeding, studying and observing birds than do the 2.5 million licensed waterfowl hunters of North America. If the bird-watching public could be enumerated and surveyed and their expenditures identified and taxed, as has happened to hunters, the conservation of migratory birds in North America would receive a tremendous impetus. At present it is still the hunters who are providing most of the revenue for the acquisition of habitat and much of the money needed to support research and public education programs.

Despite the slowly broadening scope of government administrative agencies in North America, there is increasing conflict between the "conservationists" and the "preservationists" in the public as a whole. It is rather startling and unnerving after a lifetime of working for and caring about birds to be branded as a killer because one works for a government agency. We are viewed as being unconcerned about the welfare of the birds. Unfortunately for some, ornithologists in museums and universities are being included as part of the killer "establishment".

We have attempted to describe the scale of the apparatus of waterfowl management in North America, as well as its dominance over the numerically smaller forces working for bird conservation in general. We have not yet dealt with what the apparatus is used for. Had the answer been clearer, we would doubtless have devoted the whole of this review to it; but the fact is that there are no generally-accepted objectives of waterfowl management except for the vague notions of keeping the number and distribution of the major quarry species much as they were 20–30 years ago. Several attempts have been made to define population goals for waterfowl as a whole and for some species of special interest, such as the Mallard, the Canvasback and various stocks of Canada and Snow Geese. The attempts have not led to much improvement in the effectiveness and efficiency of management, chiefly, we suspect, because there are so many different interests involved, many of them conflicting and even more of them ill-defined.

The agencies within government which control budgets are demanding evidence of purpose and effectiveness. So are various public interest groups, who question the value and purpose of the refuge systems, of the regulation of waterfowl hunting and of scientific collecting. Some of the questioning stems from hostility to hunting of any kind. From the other side, some of the powerful hunting organizations argue that there is too much

government interference. For example, the U.S. Fish and Wildlife Service has been heavily attacked for its program for outlawing the use of lead shot in areas where lead poisoning is believed to be an important cause of avoidable mortality.

Because of these pressures both the U.S. Fish and Wildlife Service and the Canadian Wildlife Service have embarked on the preparation of national waterfowl-management plans. The American plan is, we understand, now very close to its final version. The Canadian plan will, we hope, be completed this summer. After that the two agencies will attempt to build a continental management plan, involving Mexico too, if the Mexican government is willing to commit the necessary resources. Our impression is that the construction of a continental plan is going to be much harder than its proponents suppose and that to secure its acceptance and implementation will be difficult, both politically and technically.

The hard core of the management problem is this: many of the ducks that American hunters depend on are produced on privately owned farmland in the Prairie Provinces of Canada, where the small wetlands and associated nesting cover that the ducks require are seen as impediments to efficient farming. In many places the ducks themselves – especially the Mallard and Pintail – are seen as expensive nuisances, because they feed on and spoil swathed wheat.

American hunters demand a sustained or increased supply of ducks. Many of them actively seek to assure their supply by contributing to Ducks Unlimited, a remarkable organization that raises funds from waterfowl hunters – more than $ 12 million annually in recent years – to be spent, mostly in Canada, on maintaining or improving wetlands for duck production. Ducks Unlimited is now 40 years old. Its small-scale work in earlier years was welcomed by farmers in the drier parts of the prairies, where many useful stock-watering ponds were created and the building of control structures helped to keep water on the land in late summer. Now, with much more money available, Ducks Unlimited is finding it harder to combine doing good for ducks with doing good for farmers.

At the same time, expenditures by the Federal or Provincial governments in Canada to preserve wetlands for ducks are unpopular and impracticable, for two principal reasons. First, the breeding ducks are dispersed so widely that enormous areas of land are involved. As most of the land is privately-owned and producing human food crops, large-scale government intervention to intensify duck-production is politically unacceptable and financially impossible. Second, in most parts of Canada the supply of waterfowl is more than enough for Canadian hunters, summed up in a phrase about Saskatchewan, where "they don't hunt ducks, they shoot them". Why therefore should Canadian taxpayers subsidise the production of more ducks? In 1976 Canadians took about 25 percent of the North American kill of ducks and geese, yet raised 80 percent of the fall flight. Some species of ducks migrate early and are generally unavailable to Canadian hunters. Expressions of concern between managers in the two countries are generally directed at the larger forms of *Anas* and the diving ducks. The main management thrusts are being directed toward the most heavily hunted species such as Black Ducks *Anas rubripes*, Mallards, Canvasbacks, and the geese. Although the number of Canadian hunters is rising faster than that of the American hunting community, their proportion of the continental duck kill has remained largely unchanged since 1968. The kill in Canada has increased by

25 percent since 1968, largely directed at those late-migrating species also greatly prized by American hunters. At some point, possibly within the next decade, difficult decisions will have to be made about the apportionment of the kill by species and populations of species, between the two countries.

Thus the key waterfowl-management question is not simply one of biology but of economics and biopolitics: how can it be made financially worthwhile for Canadian prairie farmers to substitute the production of enough ducks of the right species for American hunters to shoot in the United States for the production of cereal grains? At this point it becomes apparent that North American waterfowl management is now too big a business to be left solely to biologists. The demand for greater and greater precision in data collection and analysis to meet international obligations, to make ecological impact assessments, and to defend their actions against the preservationists, may inadvertently once again tend to render the game-bird ornithologists inward looking. We hope not. We must not return to the two solitudes.

Techniques to Improve Nesting Success in Birds

Gustav A. Swanson

Introduction

The usefulness of artificial sites to improve nesting success in birds is reviewed for North America. Similar techniques for raptors have been discussed by several authors in the proceedings of recent symposia edited by Hickey (1969), Hamerstrom et al. (1974), and Chancellor (1977).

A recent publication (Scott et al., 1978) summarizes widely scattered information on 85 species of cavity-nesting birds of North American forests. A collection of papers on management techniques for threatened and endangered birds (Temple, 1978) will be a particularly valuable source. A book on conservation and management of nongame birds now in preparation will treat the general subject in greater detail (Swanson & Ryder, 1979). I thank Professor Joseph J. Hickey for his contributions of information and references for this review.

I select several species of North American birds which illustrate that providing artificial nesting sites has aided the populations significantly. From these some conclusions will be drawn.

Osprey *Pandion haliaetus*

The Osprey's adaptability in nesting on artificial sites has been described by many authors, including Henny (1977), Postupalsky & Stackpole (1974), and Reese (1977). In the Chesapeake Bay area 58 percent of 285 platforms built for the Ospreys were used, and less than a third of the Ospreys there were found nesting in natural tree sites, the remainder using old duck blinds, channel markers, and other structures including the platforms which had been provided especially for them. A higher nesting success was found on the man-made sites than for those nesting in trees.

American Kestrel *Falco sparverius*

The American Kestrel responds particularly well to nest boxes. Hamerstrom et al. (1973) maintained 50 nest boxes for five years on a large study area, and Kestrels using them successfully fledged 204 birds in the five-year period, while natural nest sites on the same 50,000 acre area produced only five young. Stahlecker & Griese (1978) maintained 25 Kestrel nesting boxes in eastern Colorado, placed on power lines in a grassland area, and in the third year had 24 of 25 boxes occupied by Kestrels, with one of the boxes producing two broods of young.

Snowy Egret *Leucophoyx thula* and other Ardeidae

The most successful American egret management project is "Bird City" at Avery Island, Louisiana, established by E. A. Mcilhenny (1934). In 1892, when he began his experiment with eight fledgling Snowy Egrets, the species, like other colonial nesting

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egrets and herons, had become seriously threatened with extinction through commercial hunting for their plumes, then much used in the millinery trade.

His management measures included: (1) Providing large nesting platfroms about six feet above the surface of an artificial lake. (2) Fencing and protecting from human disturbance the lake where the birds nested. (3) Providing the birds with twigs and sticks for building their nests. (4) Introducing alligators to control such nest predators as the raccoon.

By 1912 the population of several species of egrets and herons on the artificial nesting platforms had increased to 22,204 nests. The project has been maintained successfully to the present time by McIlhenny descendants, but we do not have a recent accurate count of the population. Only a few other efforts in North America to provide similar artificial nesting sites for colonial egrets and herons have been successful.

Burrowing Owl *Speotyto cunicularia*

The Burrowing Owl nests underground in burrows usually dug by prairie dogs (*Cynomys* spp.) or other burrowing mammals. COLLINS & LANDRY (1977) described the general decline in numbers of the owl and attributed it to reductions in numbers of the prairie dogs and ground squirrels (*Citellus* spp.) as a result of control programs for these rodents. This relationship is discussed more fully by ZARN (1974).

COLLINS & LANDRY prepared artificial underground burrows in the form of tunnels constructed of plywood, with a 4 x 4 inch entrance and a length of approximately 6 feet, including a right angle turn to maintain the nest chamber at the end in darkness. The burrow was buried to a depth of only 6 inches, and was equipped with an opening which made it possible to retrieve the young owls for study. Of 30 such artificial burrows installed during the 1974 to 1976 seasons 20 were in use by the third year.

Puerto Rican Parrot *Amazona vittata*

The decline of this endangered species is attributed by SNYDER (1978) to a lack of good nesting sites, and competition by the Pearly-eyed Thrasher *Magarops fuscatus*, a hole-nesting mimid, which invaded the parrot's range 25 years ago and has taken over most of its nesting holes. The successful solution (SNYDER & TAAPKEN, 1978) has been to provide artificial nesting boxes in traditional parrot nesting territories. In 1976 and 1977 all breeding parrots occupied either artificially created, or artificially modified sites, and the prospects for their survival are greatly improved.

Cliff Swallow *Petrochelidon pyrrhonota*

The account of a managed Cliff Swallow colony by BUSS (1942) described growth of the colony on a barn in southern Wisconsin from a single pair of birds in 1904 to more than 2,000 nests in 1942. The landowner, Cory Bodeman, developed a successful plan of management which included these features: (1) Control of House Sparrows *Passer domesticus*, the most important adverse factor, was accomplished by two means. Whenever possible, intruding sparrows were shot with .22 caliber cartridges loaded with small shot. Since the sparrows would use the gourd-shaped swallow nests for roosting in the winter, and for nesting in the early spring before the swallows returned, the main control of sparrow was to destroy the swallow nests in autumn, after the swallows had

departed. This also helped to control the ectoparasites, chiefly mites, which can overwinter in the nests. (2) Mud was supplied at the site for the swallows to use in building their nests. (3) A firm base for the nests and protection from the weather were provided by placing unpainted, horizontal boards on the side of the barn, and adding special "eaves" for protecting the growing numbers of nests for which there was not room under the normal eaves of the barn. (4) Cats were eliminated, because they were able to capture the swallows on the ground when occupied in gathering mud for their nest building, and also when they were competing for possession of a favorite nest site. Under such circumstances they frequently struggle so vigorously that they flutter to the ground where they are easy prey to cats.

Tree Swallows *Iridoprocne bicolor*

Many Tree Swallow nesting box projects have been conducted in various parts of the country, and we select two to illustrate how well these swallows respond.

At the Oneida Lake Biological Field Station of Cornell University near Syracuse, New York, 1955 through 1964 the number of nesting boxes for Tree Swallows was increased gradually from 7 to 160, and the nesting bird population on the 400 acre area using these boxes increased from 7 to 153 pairs (Swanson & Ryder, 1979). In the mountains of Colorado west of Denver Professor Robert Cohen initiated a Tree Swallow experiment placing nest boxes as follows: 1975–360, 1976–379, and 1978–382. The number used by the Tree Swallows each year was 89, 180, and 200 respectively. Many of the boxes were used by five other species of hole-nesting birds.

Purple Martin *Progne subis*

In the eastern part of the United States Purple Martins, probably more than any other North American bird, have become virtually dependent upon nest boxes supplied by man, and the population appears to have increased tremendously as a result. It is curious and puzzling, however, that in the western part of the United States martins still use natural cavities to the exclusion, or nearly so, of man-made martin boxes.

Even before Europeans arrived in North America Purple Martins in the eastern part of the continent were relying upon man to some extent for their nesting sites, for there is evidence that the Indians hollowed out gourds and hung them for martin nesting houses.

Soon after their arrival in North America European white men, probably inspired by the Indians, began to provide nesting sites for Purple Martins, for Catesby wrote about it in 1731. The practice has been extended and the Purple Martins have adopted the multiple-room houses to such an extent that for the last 50 years the nesting of martins in natural cavities has been very rare in the eastern half of the United States. There is no estimate to my knowledge of the number of martin houses in use, but they must number in the tens of thousands, and probably 99 percent of the Purple Martins in the eastern United States and Canada are produced in man-made houses.

Quantitative records of martin nesting success are few, but some summaries in Allen & Nice (1952) indicate the potential. A census in 1940 of the nesting Purple Martins in Ann Arbor, Michigan, revealed 22 active colonies in 37 houses which contained 761 rooms. The number of nesting pairs was 191 (23.5 percent of the rooms available).

At Baldwin, Georgia, a householder had 74 gourds for martins, and all were occupied. In another remarkable case on an estate near Chazy, New York, between 250 and 300 pairs occupied one giant house.

MAYFIELD (1969) summarized 15 years' data from the Toledo, Ohio, area, where 16-room houses were used. From 18 to 28 of the houses were used by martins each year, producing 100 to 300 or more broods of young.

ALLEN felt that in pre-European days in eastern North America the Purple Martins were certainly not as colonial as they are now, because when they were confined primarily to natural nesting sites large colonies would not have been possible.

The adverse factors preventing maximum nesting success include, according to ALLEN & NICE, weather, insect parasites, predators, and competition for nests with other birds, especially Starlings *Sturnus vulgaris* and House Sparrows. Allen & Nice considered these factors in some detail. Methods for controlling them are suggested in a popular book by LAYTON (1969).

Bluebirds *Sialia* spp.

The three species of bluebirds found in North America are all cavity nesters, and all respond extremely well to bird houses provided for them. The number of available natural cavities dug out by woodpeckers is limited, and many of them are used by the introduced House Sparrows and Starlings.

Frequently extreme winter conditions in those parts of the country where the bluebirds spend the winter have caused severe mortality, and this has stimulated efforts to do everything possible to increase the bluebird populations. The most obvious, of course, is to provide bird houses, and literally thousands of them have been placed in planned "bluebird trails".

The most comprehensive source of information is by ZELENY (1976). "Bluebird Trails" consist of Starling-proof bird houses placed at intervals along rural roadsides, usually on fence posts. They are examined periodically to determine success or failure, and to destroy the nests of competing House Sparrows. The first such "trail" was in 1934 in Illinois (MUSSELMAN, 1935) but now they are widespread over the United States and Canada, often maintained by youth groups. ZELENY (1976) has summarized their extent and success, and provides annual summaries. In 11 years of bluebird trails in the Virginia-Maryland area he estimated that more than 23,000 bluebirds had been fledged. His summary for 1977 of nearly 3,000 boxes maintained by 84 collaborators in the same area revealed that 5,357 young Eastern Bluebirds were fledged.

The largest bluebird trail project was initiated in 1959 near Brandon, Manitoba, Canada, by Dr. and Mrs. JOHN LANE. Both Eastern und Mountain Bluebirds are found in the area. By 1977 the number of bird houses placed was 4,750 scattered along more than 1,600 miles of rural roads. In 1977 reports for 941 of the boxes revealed the following nestings: Mountain Bluebird – 405, Eastern Bluebird – 33, Tree Swallow – 397, House Sparrow –166, House Wren – 48, others – 18.

Conclusions

Many other examples could be cited, but these enough to provide the basis for

generalizations. (1) There are many situations in which all other requirements are available, but lack of nesting sites is the limiting factor for some species of birds. In such situations the population can sometimes be greatly increased by providing nesting sites artificially. (2) It sometimes takes several years for the establishment in a population of birds of a tradition to accept and use artificial nesting sites. (3) Management measures may be needed and developed for individual situations to solve other problems. Examples are control of predators and competing species, control of nest parasites, and providing nesting materials.

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The Potential of Captive Breeding to Save Endangered Bird Species

S. Dillon Ripley

Introduction

While captive breeding of animals has a history as old as mankind's efforts to keep creatures captive, it is only within the last hundred years that any concerted effort has been made to keep pairs together and encourage rearing of species. Indeed only since World War I has any major effort been made to rear bird species scientifically, aside from fowl under domestication or cage birds for the pet trade. The highest refinements of what is now recongnized as an activity requiring special skill and training are only beginning to be appreciated. As this field of research develops we may approach a new era of understanding of biological reproduction, of the transfer of heterozygosity and of the preservation or loss of genotypes.

History of aviculture

Aviculture or the keeping of birds in captivity dates from the dawn of civilization. Palace parks or residences have contained captive birds since earliest times, kept for food, ornament, or for companionship as pets. Captive breeding in such cases was fortuitous, and the keeping of rare animals was for prestige, either of the powerful individual or the zoo, with no thought of conservation of the genotype until very recently. Among birds, the Hawaiian Goose *Branta sandvicensis* and the Brown Eared Pheasant *Crossoptilon mantchuricum* were imported and breeding was attempted consciously in aviaries early in the Nineteenth Century. In this century, the Imperial Pheasant *Lophura imperialis* and Edwards's Pheasant *Lophura edwardsi* are known only from aviary specimens (Delacour, 1951, 1954).

Present history

The potential of captive breeding to save endangered species of birds is perhaps best realized by an experiment in the United States of America which has still received little notice, the saving of the Wood Duck *Aix sponsa*. The fascinating story of how this beautiful bird was brought back from the verge of extinction by the efforts of a few dedicated men is one that is recounted in detail in several of my publications (Ripley, 1951, 1957, 1973).

To the conservation organizations of the time, such as the National Audubon Society, a program of captive rearing of an endangered bird species, such as the Wood Duck, was distasteful. This reluctance to consider birds in captivity as possessing the same precious genes as their conspecific species-members in the wild state hindered the possibility of aviculture as a partner in conservation. The very conservationist organizations which should have been grasping at any and all scientific measures for the preservation of a

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species, equally and clearly, were biased against captive rearing as a possible tool. This technique is in fact equal in importance to refuge development or the preservation of national parks.

A recent well-publicized effort with a species of waterfowl has been the reintroduction of the Hawaiian Goose to its old range on the main island, Hawaii, and on Maui Island of that Archipelago. The background story has been told several times (Ripley, 1965; Zimmermann, 1975).

Another important bird of Hawaii, saved by captive rearing, is the Laysan Teal *Anas laysanensis* of Laysan Island, a two-mile raised coral islet of the Leeward Chain, 800 miles northwest of Honolulu. The decline of this species and its reemergence is a cause of biological concern, and prompted me to intercede with the U. S. Government in 1956, hoping to establish a buffer population in captivity. I have written of the species (1959), and the present history, including the extraordinary speculation that the entire world population may have arisen from a single gravid female, inseminated by a subsequently deceased male, who renested and reared a second clutch of eggs in 1930 (Zimmerman, 1975), is a story which almost defies belief.

The account of the decline of the Whooping Crane *Grus americana* of North America has been recently well summarized by McNulty (1966). What is now happening a dozen years later has been derived from a variety of experience, involving further field studies, captive behaviour, reproduction, survival rates and planning based on a complex of new data. What is significant today, in 1978, is that a whole new field of avicultural management is gradually being developed. Where 20 years ago there was general doubt among biologists as well as conservationists about the potential of captive breeding of endangered species, the new field of manipulative aviculture is most encouraging.

What is manipulative aviculture? From a physiological point of view, the basic understanding of artificial insemination which has emerged is the primary tool for such work. Beginning two years ago with the first breeding of the Neotropical Ocellated Turkey *Meleagris ocellata* in captivity, the technique has been developed particularly with raptors (Gee & Temple, 1979) and with cranes, with the work of the Endangered Species unit of the Fish and Wildlife Service at Patuxent, Maryland, and now with the International Crane Foundation at Baraboo, Wisconsin. In the latter location Dr. George Archibald and his colleagues have been able to produce viable eggs and rear young from cranes of nearly 50 years of age, individuals that have never been known to breed in captivity previously. A female Japanese Crane *Grus japonensis*, at that age, kept in proximity to an arthritic male, both bird pensioners at different zoos, displayed and danced, aided by inciting behaviour by the Crane Foundation's staff, eventually ovulated, and the male produced viable semen, for successful artificial mating three years in a row.

It has been my own hope for twenty years that the United States officials in charge of migratory birds, the U. S. Fish and Wildlife Service, would attempt to develop a resident flock of Whooping Cranes in the lower Mississippi flyway. Based on the certain knowledge that a non-migratory flock formerly existed in the central part of the southern United States, it seems to the International Crane Foundation as well as to myself (for I have been writing about this since the late 1950s) that an eventual settling of birds in the lower Mississippi flyway area on one of the present tracts of federally-owned land within a large fence enclosure, would be fruitful and productive. Experience with breeding cranes in

captivity shows that the migratory instinct is not dominant among birds reared in captivity. Thus wing-clipped birds might be released in a large penned enclosure and allowed to fly out gradually as their wings developed. Such birds tend to be associated with their home place in the same way that a flock of Canada Geese similarly released will tend to stay put without migrating if water and food conditions are appropriate. A proposal to this effect has recently been sent in to the Fish and Wildlife Service by the International Crane Foundation, and endorsed by a number of those interested in captive rearing as an effectice management technique. It is our hope that favourable action will be taken sometime in the near future.

Some of the most spectacular manipulative aviculture has been practised with the raptors, falcons, hawks and eagles. In the United States the primary work has been performed by Professor Tom Cade and his circle at Cornell University. Dr. Cade's work on the Peregrine *Falco peregrinus* has been summarized in a number of articles in the newsletters of the Peregrine Fund (1973–1975). Long-vacant eyries in the eastern United States have been painstakingly repopulated with captive-reared fledglings over three seasons, with every indication that these birds, released and monitored by close observation, are capable of feeding themselves independently some seven weeks after being allowed to fly free. In addition to the Peregrine, extirpated in the eastern United States and much of eastern Canada by organochlorine residues, the Prairie Falcon *Falco mexicanus* of the central and western States is now being reared in Colorado for eventual release to old eyries. This project demonstrates a very high degree of successful manipulative techniques including the whole process of breeding in captivity, rearing the young from eggs, fledging and feeding and monitoring the release to its free, independent conclusion, a program which would have been unimaginable a few years ago.

With eagles a modified technique has been developed of introducing viable eggs from wild or from captive nests into persistent nests of wild breeders, crippled by a pesticide overload and thus prevented from laying hatchable eggs on their own. This spring (1978), in the eastern United States two captive-reared juvenile Bald Eagles *Haliaeetus leucocephalus* are being introduced directly into the nests of nonsuccessful pairs with immediate adoption taking place (one has subsequently developed cataracts and will probably not be used). There seems no reason to believe that similar technical achievements could not be accomplished with the remaining breeding eagle populations of Europe and Asia, where successful captive breeding may occur, hopefully with Steller's Sea Eagle *Haliaeetus pelagicus,* hopefully in Berlin, East Germany or Japan; or the Monkey-eating Eagle *Pithecophaga jefferyi* in the United States or Belgium.

Future prospects

The potential of captive breeding to save endangered bird species is still an open question in some ways. I believe it is better in all cases to be optimistic only to be proved wrong later, than to start off being pessimistic, only to be proved right (or wrong) after some time. There are too many pessimists or wiseacres in the world at any one time. Thus I feel that in the past, conservation organizations in the United States through their distaste or timidity helped to inhibit captive breeding programs which have later succeeded (*vide* the Whooping Crane already cited). That timidity, State chauvinism and personal hostility have prevented any avicultural management for the fast-diminishing population of

California Condor *Gymnogyps californianus,* seems beyond question. It may be too late to save the last individuals, although at the eleventh hour a Condor Recovery Team, of Federal, State and conservation organization members, has been created. If the remaining individual condors are largely senescent (only one young was produced last year), or newly infected with organochlorines or persistent chemical systemic residues, the valiant efforts and the high hopes of all of us may be finally frustrated. And yet it is better to try and fail than never to have tried at all.

Complaints against aviculture have been raised that in the case of severely limited or endangered populations close inbreeding is bound to be unsuccessful because of inherited lethal or harmful genes. Examples abound, however, in mammals at least of the possibility that this is not always a valid argument, witness the golden hamster and Père David's deer. That highly-evolved warm-blooded vertebrates are capable of similar luck in the genetic sweepstakes would seem to be proved by the case of the Laysan Teal already cited.

What then are the prospects? At present there are 424 taxa in the revised Red Data book, compiled by the International Council for Bird Preservation for the International Union for the Conservation of Nature (1978, in press). Of these species 77, often represented by subspecies, have bred in captivity, representing 18.1% of the total. This figure could be greatly increased, as has been shown with the Pink Pigeon *Columba mayeri* of Mauritius, now recently brought into captivity and breeding for the first time in history.

There is a legend that ravens must be kept alive, living in the Tower of London, lest the British monarchy fail to survive. The concept of species of birds, that wonderful wild, winged class of animals surviving only in parks, small selections of biotope, menageries of wildness of the future, sends shivers down the backs of all bird lovers. But meanwhile let us not lose hope, not assume that aviculture is a plot to create such triumphs of artificiality, under the guise of maintaining a reservoir of genetic variability. Birds must continue to exist by whatever means are available, and the new systems to be derived from human skills at manipulation are only the very least that we can do, who have all but destroyed a very large segment of our natural environment.

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Organochlorine Contamination of the Peruvian Coastal Ecosystem: Baseline Levels in 1969

Robert W. Risebrough

Introduction

In this paper we present the results of a study of organochlorine contamination of the Peruvian coastal ecosystem that was carried out in 1969. The results remain of interest for diverse reasons, but principally because:

(1) the populations of the three most abundant among the species of guano birds, the Guanay *Phalacrocorax bougainvillii,* the Piquero *Sula variegata,* and the Alcatras, or Pelican peruano, *Pelecanus thagus,* declined sharply in numbers after the 1965 El Niño (Jordan & Fuentes, 1966) but, contrary to the pattern of population recovery following previous Niños, their numbers remained low throughout the remainder of the decade. The populations were further reduced, to levels that probably represent an all time low, after the El Niño of 1972 (R. Jordan, personal communication; Idyll, 1973);

(2) the data constitute baseline values for future Peruvian investigations of local environmental contamination and for investigations carried out in neighbouring countries;

(3) they provide comparative organochlorine residue data from a year when populations of related species in North America were experiencing extensive reproductive failures associated with eggshell thinning;

(4) they indicate levels of coastal contamination in a developing country rapidly expanding both its industrial and agricultural economies;

(5) they provide an indication of high levels of organochlorine contamination in an Andean Condor *Vultur gryphus.*

The majority of the samples were obtained in December, 1969, in various coastal Peruvian localities. A sample of body fat from an Andean Condor was obtained in January, 1970. In addition we present the results of the analysis of eggs of the Brown Pelican obtained in Venezuela and Jamaica in 1969. Residue values in eggs of this species from the Galapagos Islands, Panama, Mexico and the United States are also presented in order to provide a picture of comparative contamination levels of DDT and PCB compounds in North and South America at that time.

The sampling of the various components of the food web in coastal Peru was based largely on the model provided by Hedgpeth (1957). In addition to the bird eggs, sea lion tissues, and fish, samples of the alga, *Fucus* sp., jellyfish, sea urchins, intertidal and deep-water snails, shallow-water clams, sand and littoral crabs were obtained.

Materials and methods

Whole eggs, whole fish or portions of fish, and muscle tissues of the sea lion *Otaria flavescens* were weighed in the field; these samples, and the body fat sample from the

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TABLE 1. DDT and PCB levels in birds, sea lions and fish from coastal Peru in 1969 and early 1970. Mean percent lipid and parts per million of the lipid weights.

Species	Locality	Date	Tissue	No.	DDE	Total DDT	PCB	Percent* lipid
Birds								
Pelicano, *Pelecanus thagus*	Isla Vieja	17 Dec.	egg	5	4.3	4.9	12	4.3
Guanay, *Phalacrocorax bougainvillii*	Isla Vieja	17 Dec.	egg	4	12	ND**	15	3.1 (2)
Piquero, *Sula variegata*	Isla Santa Rosa	17 Dec.	egg	1	20	ND	22	3.7
Pinguino de Humboldt, *Spheniscus humboldti*	Moro Quemado	18 Dec.	egg	2	6.0	ND	15	5.8 (1)
Gaviota dominicana, *Larus dominicanus*	Moro Quemado	17 Dec.	egg	5	28	28	31	8.1 (2)
Gaviota peruana, *Larus belcheri*	Moro Quemado	18 Dec.	egg	3	23	ND	22	5.2
Condor, *Vultur gryphus*	Moro Quemado	22 Jan. 1970	body fat	1	320	330	370	ND
Mammals								
Lobos marinos, *Otaria flavescens*	Moro Quemado	18 Dec.	muscle, flipper	3	5.5	ND	17	2.5
	Playa de las Salinas	14 Dec.	muscle, flipper	1	11	ND	62	0.9
	Lagunillas	13 Dec.	muscle, flipper	1	3.5	ND	7.8	2.0
Fish								
Anchoveta, *Engraulis ringens*	Paracas	20 Dec.	Whole fish[a]	5	0.030	0.064	0.45	9.9
Sardina peruana, *Sardinops sagax*	Pisco	14 Dec.	x-sections[b]	5	1.0	1.2	0.64	2.2
Caballa, *Scomber japonicus peruanus*	Pisco	14 Dec.	x-sections	5	0.75	0.98	2.1	0.9

Species	Locality	Date	Tissue	No.	DDE	Total DDT	PCB	Percent* lipid
Bonito, *Sarda sarda chiliensis*	Pisco	14 Dec.	x-sections[b]	5	0.76	1.22	0.53	1.5
Tiburon azul, *Prionace glauca*	Pisco	14 Dec.	muscle plus skin	2	2.3	6.1	11	0.68
Pejerrey, *Odontesthes regia regia*	Pisco	14 Dec.	x-sections	5	2.3	3.6	9.6	0.35

* Weight of shell included in fresh weight determinations of eggs; numbers in parentheses indicate samples sizes of lipid percentage determinations if different from N.
** ND, Not determined.
[a] mean weight and length: 18.3 gm and 13.0 cm [b] ¼ inch x-sections, immediately anterior to the anus.

TABLE 3. DDE and PCB residues in cormorants, *Phalacrocorax* spp. Parts per million of the lipid weight; geometric means.

Locality, date	Species	N	Tissue	PCB	DDE	PCB/DDE
Amchitka, 1971 (1)	*P. urile*	1	Egg	19	3.8	5
Amchitka, 1974 (1)	*P. urile*	1	Pectoral muscle	21	3.5	6
Agattu, 1974 (1)	*P. urile*	1	Pectoral muscle	14	2.4	6
Amchitka, 1974 (1)	*P. pelagicus*	1	Pectoral muscle	8	0.8	10
Auckland Islands, 1972 (2)	*P. campbelli*	4	Egg	0.3	0.9	0.3
Iceland, 1973 (3)	*P. aristotelis*	10	Egg	23	3.8	6
	P. carbo	13	Egg	10	3	3
Peru, 1969 (4)	*P. bougainvillii*	4	Egg	15	12.2	1.2
Southern California, 1969 (5)	*P. auritus*	7	Egg	87	754	0.1
Greenland, 1972 (6)	*P. carbo*	3	Body fat	23	9.8	2.3

(1) WHITE & RISEBROUGH, 1977. (2) BENNINGTON et al., 1975. (3) SPROUL et al., unpublished manuscript. (4) This paper. (5) GRESS et al., 1973. (6) BRAESTRUP et al., 1974.

Andean Condor, were ground in the field with anhydrous sodium sulphate and wrapped in aluminium foil for transport to the laboratory. The analytical methodology employed has been described by Risebrough et al. (1970).

Results

Results of the analyses are presented in Table 1. Organochlorine residues in the invertebrates and in *Fucus* were found to be very low, at the background levels, or lower, of the sampling and analytical procedures employed. The results of those analyses are not therefore reported.

The highest levels were recorded in the body fat sample of the Andean Condor, 320 ppm DDE and 370 ppm PCB, lipid weight. Whether this particular bird had been exposed to exceptionally high levels of contamination in its food, or whether this species accumulates, because of the nature of its metabolism, higher levels of organochlorine pollutants than other species is unknown. This result is of interest, however, since high levels of DDE have recently been found in tissues of the related California Condor *Gymnogyps californianus,* which have been associated with shell thinning in that species (Kiff et al., 1979). Lower reproduction of the California Condor in recent years may therefore have been caused, at least in part, by the DDE-thin eggshell syndrome. Whether the Andean Condors in Peru are similarly endangered evidently requires further investigation.

The DDE and PCB contamination levels in the Peruvian pelicans are compared in Table 2 with data obtained from the closely related species *P. occidentalis* in other South American localities, Panama, Jamaica, Florida, western Mexico, and southern California. The lowest levels were recorded in the Galapagos pelicans; except for minor DDT use, input of these pollutants into the Galapagos environment would appear to be low. Contamination levels in Peru, Panama, Venezuela and Jamaica were all approximately comparable in that time period and were all considerably lower than residues in the Florida eggs. The exceptionally high levels in southern California and northwestern Baja California have been attributed to a local industrial discharge in Los Angeles (Anderson et al., 1975) and decreasing levels of both DDE and PCB were observed from north to south in western Baja California (Table 2). Pelicans breeding in the Gulf of California are known to migrate after the breeding season to coastal California (Anderson & Anderson, 1976). Most likely the DDE recorded in the pelican eggs in the Gulf of California in 1970 and 1971 derived principally from Californian rather than from Mexican sources.

Comparable data for cormorants of the genus *Phalacrocorax* are presented in Table 3. The Double-crested Cormorants from southern California showed the same patterns of high DDE contamination and low PCB/DDE ratios as did the pelicans. The Peruvian values are roughly comparable to those recorded in other species in Greenland and Iceland and in the majority of the samples from the Aleutians. The lowest contamination levels were found in eggs of the Aukland Island Shag; the low PCB/DDE ratios appear to be typical of the subantarctic as well as the Antarctic (Risebrough et al., 1976). The PCB/DDE ratio in the Peruvian samples is lower than that in the majority of the cormorant eggs and tissues from the Northern Hemisphere, which contained considerably more PCB than DDE.

Table 2. DDE and PCB residues in eggs of Brown Pelicans, *P. occidentalis* and *P. thagus*. Parts per million of the lipid weight; geometric (GM) or arithmetic (AM) means.

Locality, date	N	GM/AM	PCB	DDE	PCB/DDE
Peru, 1969 (1)	5	GM	12	4.3	2.8
Galapagos Islands, 1970 (2)	6*	GM	0.2	0.5	0.4
Islas Perlas, Panama, 1968 (3)	6	AM	4.5	7.9	0.6
Venezuela, 1969 (1)	4	AM	5.0	0.9	6
Jamaica, 1969 (1)	4	AM	19	4.2	5
Florida, 1969 and 1970 (4, 5)	87	AM	71	26	3
Anacapa Is., Ca. 1969 (5)	65	AM	210	1 176	0.2
Los Coronados, Baja California, 1969, 1970 (5)	28	AM	266	1 109	0.2
San Martin Is., Baja California 1969 (5)	6	AM	72	411	0.2
San Benitos Is., Baja California 1969, 1970 (5)	10	AM	39	121	0.3
Gulf of California 1968, 1969 (5)	4	AM	4	11	0.4
Gulf of California 1970, 1971 (6)	74	AM	not determined	142	—

* Two clutches. (1) This paper. (2) R. W. Risebrough, J. T. Mendola, C. W. Connors & M. P. Harris, unpublished data. (3) Risebrough et al., 1968. (4) Schreiber & Risebrough, 1972. (5) Risebrough, 1972. (6) D. W. Anderson, unpublished data. Analysed in Laboratory of Denver Wildlife Research Center.

The Peruvian samples showed a rather wide range in the PCB/DDE ratios (Table 1). Usually these ratios tend to be relatively consistent within a particular ecosystem (Risebrough et al., 1968). We attribute these differences in Peru to a variety of input sources along the coast of both PCB and DDE. The pattern of upwelling in coastal Peru is known to be irregular (Paulik, 1971); the chemical composition of the water masses is not therefore uniform. A discussion of coastal pollution problems in Peru has been presented by Reyes (1970).

In summary, coastal contamination in Peru by the DDE and PCB compounds was not markedly higher than in other South American localities in 1969—1970 and was considerably lower than in North America. As the economies of Peru and of neighbouring countries continue to expand, however, levels of contamination by these and other pollutants in coastal food webs might increase and continuing studies are warranted.

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Pollutant Levels and their Effects on Raptoral and Fish-Eating Birds

David B. Peakall

There is a feeling among ornithologists that the era of the persistent organochlorine pesticides is closing. This is only true for the northern temperate zone. The overall usage of these materials is not, according to best estimates, decreasing but the areas of major usage are moving southwards (Risebrough, 1980). Details of residue levels found in raptorial and fish-eating birds and their food in Central and South America are given in subsequent papers of these proceedings; here an overview is presented.

This symposium is an attempt to document and assess the impact of pesticides on the avifauna of the third world. The two basic questions to be answered are: what should be looked for to see whether or not pesticides are affecting the avifauna, and secondly what species should be considered as reasonable candidates for a list of those likely to be affected?

The question of what effects are to be looked for can be addressed by examination of (1) field studies of the effects of pollutants carried out on closely related species in the holarctic and (2) laboratory studies, usually on target species. Neither method is ideal. The first suffers from the fact that while the results are correlated with pollutant loads, proof of cause-and-effect is generally lacking. The second suffers from the fact that usually neither the conditions nor the species are identical to field conditions. Nevertheless a great deal of information is available, so that some reasonable assessment is possible.

The most obvious adverse effect of pesticides is direct mortality. While kills of birds have occurred with all the major classes of pesticides — organochlorines, organophosphates, carbamates — they tend to be rather localized.

Massive decreases of the population of Common Eiders *Somateria mollissima* in the Wadden Sea from 1960—1965 were considered to be due to endrin, telodrin and dieldrin (Swennen, 1972) and the same chemicals caused mortality of Sandwich Terns *Sterna sandvicensis* near the mouth of the Rhine in 1964—65 (Koeman et al., 1967).

Carbophenothion, used to treat winter-wheat, was the cause of death of some 500 Grey-lag Geese *Anser anser* in Scotland in 1971 (Bailey et al., 1972) and several hundred Green-winged Teal *Anas carolinensis* were killed by carbofuran in British Columbia in 1976 (Whitehead, personal communication). Almost certainly the most massive mortality of birds caused by pesticides has occurred in forest spray programs. In 1975 some 2.7 million hectares were sprayed in New Brunswick using fenitrothion and phosphamidon. The total mortality of songbirds was estimated to be in excess of three million (Pearce et al., 1976).

The greatest danger from a species point-of-view would be expected for those species of limited geographic range which coincide with areas of heavy pesticide usage.

It is likely that effects on reproductive success by sub-lethal levels of pesticides have had a more significant long-term effect than direct mortality. I wish to consider two aspects of pollutant-related effects on reproduction, viz, eggshell thinning and behav-

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TABLE 1. Field and laboratory studies relating physiological effects to pollutant levels in birds

Species	Type of study	Chemical	Effect observed	Residue level in egg or diet	Reference
Pelecaniformes					
Brown Pelican *(Pelecanus occidentalis)*	Field	DDE Dieldrin	Hatching failure	8.5 ppm 1.0 ppm	BLUS et al. (1974)
Great Cormorant *(Phalacrocorax carbo)*	Field	DDE	Eggshell thinning leading to breakage	10.0 ppm	KOEMAN et al. (1972)
Double-crested Cormorant *(P. auritus)*	Field	DDE	Reproductive failure	24 ppm in failing colonies, 2 ppm in successful	GRESS et al. (1973)
	Field	DDE PCB	Eggshell thinning Population declines	7—11 ppm 10—12 ppm	POSTUPALSKY (1971)
Ciconiiformes					
Grey Heron *(Ardea cinerea)*	Field	DDE	Eggshell thinning leading to breakage	25 ppm	COOKE et al. (1976)
Black-crowned Night Heron *(N. nycticorax)*	Field	DDE	Eggshell thinning leading to breakage	20 ppm	PRICE (1977)
Anseriformes					
Black Duck *(Anas rubripes)*	Laboratory	DDE	Increased embryonic mortality and decreased chick survival	10 ppm in diet 46 ppm in egg	LONGCORE et al. (1971)
Mallard *(A. platyrhynchos)*	Laboratory	DDE	As above	10 ppm in diet	HEATH et al. (1969)
Common Merganser *(Mergus merganser)*	Field	DDE PCB	Significant eggshell thinning	19.4 ppm 61.0 ppm	WHITE & CROMARTIE (1977)
Red-breasted Merganser *(M. serrator)*	Field	DDE PCB	Significant eggshell thinning	16.0 ppm 46.0 ppm	WHITE & CROMARTIE (1977)

Species	Type of study	Chemical	Effect observed	Residue level in egg or diet	Reference
Falconiformes					
California Condor *(Gymnogyps californianus)*	Field	DDE	Significant eggshell thinning and structural changes	4.0 ppm	KIFF et al. (1979)
Golden Eagle *(Aquila chrysaetos)*	Field	Dieldrin	Reproductive failure	0.9 ppm caused decreased success; 0.3 ppm not effect	LOCKIE et al. (1969)
Peregrine Falcon *(Falco peregrinus)*	Field	DDE	Eggshell thinning leading to reproductive failure	15—20 ppm	PEAKALL et al. (1975)
Prairie Falcon *(F. mexicanus)*	Field	DDE	Decreased productivity Reproductive failure	2 ppm 12 ppm	FYFE et al. (1976)
American Kestrel *(F. sparverius)*	Laboratory	DDE	Eggshell thinning leading to reproductive failure	6 ppm in diet 30 ppm in eggs	LINCER (1975)
Columbiformes					
Ring Doves *(Streptopelia risoria)*	Laboratory	PCB	Behavioral changes, decreased productivity	10 ppm in diet 16 ppm in eggs	PEAKALL & PEAKALL (1973)
	Laboratory	DDE	Behavioral changes	10 ppm in diet 41 ppm in brain	HEAGLE & HUDSON (1977)
Strigiformes					
Screech Owl *(Otus asio)*	Laboratory	DDE	Eggshell thinning	2.8 ppm in diet	MCLANE & HALL (1972)

ioral effects. The first phenomenon is well documented and readily quantified; the second is not well documented and is difficult to quantify. A range of these studies, both field and laboratory, are listed in Table 1. No attempt is made at completeness.

Eggshell thinning of raptorial and fish-eating birds has proved to be a good index of DDE levels high in the food web. Since the discovery of eggshell thinning (Ratcliffe, 1967), many studies have been made involving a considerable number of species. Studies on the Peregrine *Falco peregrinus* alone include Ratcliffe (1967, 1970), Hickey & Anderson (1968), Cade et al. (1971), Peakall et al. (1975). Eggshell thinning has been considered to be an important factor in pollutant-caused reproductive failure. Correlation of population declines (Hickey & Anderson, 1968) and experimental studies (Lincer, 1975) shows that a degree of thinning of 19—22 % is critical for raptors. The degree of eggshell thinning in the Peregrine is shown in Figure 1. The DDE levels were measured by extraction with solvents from eggs in collections (Peakall, 1974). This technique has the great advantage of being non-destructive. The number of specimens available, and the year of collection, are variable but nevertheless the data illustrate the global nature of the problem. Only a few non-migrating races, such as those in Indonesia and the deserts of Australia, do not show significant eggshell thinning. Full details are given elsewhere (Peakall & Kiff, 1979). Similar findings have been noted with the Saker Falcon *F. cherrug* where twenty-five eggs collected from 1961 to 1966 had an Eggshell Index (Ratcliffe, 1967) of 1.82 compared to a pre-1945 value of 2.11. In the Lanner Falcon *F. biarmicus* clutches collected from Orange Free State in 1959, Natal in 1963, Transvaal in 1969 and Namibia in 1976 were markedly thin whereas sets from Rhodesia in 1955, Natal in 1960 and Orange Free State in 1971 and 1972 were close to the pre-1945 value.

Twenty percent eggshell thinning, the degree considered critical, was found in 25 of 63 eggs of the Bat Falcon *Falco rufigularis* collected in Mexico between 1956 and 1967

Figure 1. Global distribution of eggshell thinning in the Peregrine Falcon. Figures are percentage reduction in Eggshell Index. Adapted from Peakall & Kiff (1979).

and in 15 out of 25 eggshells of the Aplomado Falcon *Falco femoralis* collected there between 1957 and 1966 (KIFF et al., 1980). In both cases a strong negative correlation was found between the degree of eggshell thinning and DDE levels in the membranes.

CADE (1968) commented that "down through the centuries, not all the falcon trappers, egg collectors, war ministries concerned for their messenger pigeons, or misguided gunmen have been able to effect a significant reduction in the numbers of breeding falcons. But the simple laboratory trick of adding a few chlorine molecules to a hydrocarbon and the massive application of this unnatural class of chemicals to the environment can do what none of these other grosser, seemingly more harmful agents could do". From the viewpoint of population dynamics it is more harmful to have unproductive adults maintained in their territories than to kill the breeding adults outright.

Eggshell thinning has also been well-documented within the orders Pelecaniformes and Ciconiiformes. The most dramatic case was the Brown Pelican *Pelecanus occidentalis* at Anacapa Island off the coast of California. Here eggshell thinning of up to 95 % was recorded, with the mean thinning of over 50 % (RISEBROUGH, 1972). Fortunately, the contamination of other populations of this species is much lower. The levels of DDE and PCB's in the eggs from Peru, Panama and Venezuela are some two orders of magnitude lower (RISEBROUGH, 1980) and those from the Galapagos Islands lower still.

Broken and crushed eggs of the Cattle Egret *Bubulcus ibis* were found in Guatemala (HERMAN et al., MS) and significant eggshell thinning was noted in this species in Colombia (FABER & HICKEY). The highest levels of DDE were associated with cotton-growing areas. Levels in fish were low in Colombia and Brazil (FABER & HICKEY, MS) except locally and were low from coastal areas of Peru (RISEBROUGH, 1980). While the data base is relatively limited, it does suggest that high levels of organochlorines are still relatively localized in South and Central America.

The defence of organisms against organochlorines is weak. The carbon-chlorine bond is found in nature only in a few fungi (ROCHE et al., 1963) and thus the ability to split this bond is virtually unknown. The major physiological response to organochlorines is the induction of nonspecific mixed function oxidases in the liver. These enzymes, which are induced by a wide variety of foreign substances, render the contaminant more polar and thus more readily excreted. One intriguing aspect of these mixed function oxidase enzymes is that they also increase the metabolism of hormones (CONNEY & BURNS, 1972).

This suggests the possibility of a direct link between pesticides and behavior and there are some field studies that indicate that this is occurring. MILSTEIN et al. (1970) recorded a Grey Heron *Ardea cinerea* stabbing eggs and flinging them out of the nest. FYFE et al. (1976) have found that changes in nest defence behavior of Merlins *Falco columbarius* were significantly associated with increasing levels of DDE and possibly also PCBs; more contaminated individuals were less aggressive in defending territories. Colonies of Herring Gulls *Larus argentatus* with very low reproductive success on Lake Ontario were characterized by poor nest defence, high rate of loss of eggs, and high embryonic mortality. In these failing colonies the breeding adults left the island when the approaching boat was still several hundred metres from shore; normally adults remain until one is a few metres away and some individual gulls will even attack the

investigator. The use of telemetering eggs showed that there were much longer absences of adults from the nest in the absence of human disturbance on the Lake Ontario colonies than in a successful coastal colony and consequently greater temperature variation of the eggs (Fox et al., 1978).

While definitive studies relating behavior, hormone levels and pollutant load remain to be carried out, the indication is that behavioral effects are as important as direct toxicological effects.

There is evidence that in the drier areas of Africa the distribution pattern of organochlorines may be different from that found in the Neotropics. Koeman et al. (1972b) found extremely low levels (viz a few thousandths of a ppm) of chlorinated hydrocarbon pesticides in the livers of the Reed Cormorant *Phalacrocorax africanus* collected from Lake Nakuru in 1970. The levels found by Lincer et al. (in press) for eggs of *P. carbo* collected from the same lake in 1970—1972 were much higher, viz a mean level of 0.77 ppm, and those of *P. africanus* from Lake Naivasha averaged 2.1 ppm. While these levels are below those considered critical, they are much higher than would be expected from Koeman's data. Koeman & Pennings (1970) also reported low organochlorines in fish-eating birds collected in the Chad Basin. It has been suggested (Koeman et al., 1972) that the low levels of organochlorines in the tropics in comparison to the usage patterns may be due to a high rate of volatilization and co-distillation of pesticides. Certainly there is good evidence that the aerial route is the most important one in the translocation of organochlorines (Scep, 1970) and the pesticides located in Antarctic snow (Peterle, 1969) may originate from the tropics. Direct evidence of translocation by the aerial route over thousands of kilometres has been demonstrated (Risebrough et al., 1968; Peakall, 1976). If these theories are correct then the usage of organochlorines in arid regions may well be a diffuse global problem rather than a point source problem. It could be similar to the acid rain problem where the building of high stacks overcame a local air pollution problem but created a global one.

In conclusion, I would like to propose that the major areas of pesticide usage be mapped from the files of the World Health Organization and Food and Agriculture Organization and that these data be compared with maps of the ranges of species in the Neotropical and Ethiopian regions. While neither set of maps will be precise, it should enable us to come up with a list of species that are potentially endangered from pesticide usage. Thus the Lagger Falcon *Falco jugger*, whose range is largely within India and whose habitat is described by Brown & Amadon (1968) as "cultivated plains with trees and open country . . . does not avoid human habitation", should be in much greater danger from this particular activity of man than the Osprey *Pandion haliaetus* which breeds on every continent except Antarctica.

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The Effects of Tsetse Fly Control Measures on Birds in West Africa

M. Smies

Introduction

Tsetse flies occur in most of Africa south of the Sahara over an area of approximately 10 millions km^2, roughly twice the area of Europe. It is generally thought that the occurrence of tsetse fly as transmitters of diseases has greatly impaired human development in Africa.

Tsetse fly control has been carried out by various means since the beginning of this century but presently utilizes insecticides. Systematic research into the environmental effects of tsetse control operations has been carried out since 1969. This paper reviews the results of this research so far as it deals with effects on birds.

The Tsetse Fly

Tsetse flies are now confined in their distribution to the African continent. Some twenty-two species are involved, all placed in the one genus *Glossina* and closely adapted to a range of habitats from savannah to tropical rain forest. It is rare for more than three or four species to coexist. Their main environmental requirements are:

(1) food, both sexes of the fly require a vertebrate blood meal at regular intervals; (2) vegetation, providing humidity, shade and resting places for the fly; (3) soil, which must be of the right type and humidity to provide the larvae with a site for their puparial development. The dominant climatic factor is temperature, which must be between ca. 16 and 40°C.

For insects, tsetse are unusually long-lived (up to 100 days) and have a low reproduction rate (one larva per 12 days per female). The flies can exist at very low population densities, equal to or even below the limits of detection by present survey methods.

Tsetse borne disease

The tsetse fly's dependence on vertebrate animals has been exploited by protozoan blood parasites of the genus *Trypanosoma.* These mature in the vertebrate host but pass through a cyclical development in the tsetse. The indigenous game of Africa appears to be tolerant to *Trypanosoma* infection but man and his domestic livestock suffer disease: sleeping sickness in man, nagana in cattle.

Gambian sleeping sickness tends to be a more chronic, debilitating condition than Rhodesian sleeping sickness, which is acute and often fatal. Nagana is carried by wild hosts and is chronic or acute depending on the type of trypanosome and the sensitivity of the domesticated host. All trypanosomiases can be cured by pharmacotherapy, but this is usually only successful in the early stages of the disease and resistance of trypanosome strains to a number of drugs has developed.

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Tsetse control

Control of trypanosomiases has been motivated by anthropocentric reasons — to protect man in the first instance and his livestock in the second. Because of the practical problems with direct control of the disease, such as the need for regular diagnostic checks, the impracticability of effective prophylactic treatment and the occurrence of drug resistance, most effort has been devoted to attempts to break the transmission cycle of the disease by control of the tsetse fly.

From earliest times, man's knowledge of the tsetse fly's ecology has been utilized in devising control procedures. "Fly-belts", areas suitable for tsetse in the drier regions, were recognized early and there bush clearance was undertaken where feasible, thus depriving the flies of their required micro-climatic conditions. The destruction of the fly's food sources, i.e. of game, was also undertaken. Although both these methods could be refined as man's knowledge of fly behaviour and host preferences increased, it is hardly surprising that, when versatile and potent insecticides became widely available, their potential for tsetse control was quickly evaluated. Compared with many developments, this evaluation was always based on man's insight into the pest's ecology. The ecological aspect particularly exploited was the resting site of the tsetse. This represents a small part of the fly's habitat, but covering it with a residual deposit of insecticide would break the life cycle of the fly and the transmission cycle of the fly-borne diseases.

Various methods of control have been developed, employing both ground and aerial residual application of insecticides and repeated aerial application of aerosol droplets to control the adult fly.

Environmental impact of Tsetse control operations

Both tsetse control operations and the associated human land utilisation exert effects on the natural environment. Former control techniques, such as bush clearing and game destruction, have an obvious direct environmental impact. Present tsetse control operations, whether utilising ground or aerial spraying, require some ground access to the area being treated. This enhances the possibilities for subsequent settlement and indeed such settlement is often desirable from the tsetse control point of view as it renders the habitat less suitable for tsetse fly and thereby protects the area against re-infestation (Davies, 1977).

Ideally, environmental impact research should cover both the tsetse control operation itself and the ensuing rural development, but until now it has dealt mainly with the tsetse control operations and in particular with the effects of insecticides. The reasons for this restricted approach were partly historical in that it was a logical extension of research into the environmental effects of insecticides in the temperate regions.

Experience in Nigeria

In West Africa by far the largest tsetse control programme has been carried out in Nigeria. Large scale operations started about twenty years ago in the North of the country to protect the cattle of the nomadic herdsmen (Fulani) on their north-south journeys following the onsets of the dry and wet seasons. Control operations are car-

ried out in the dry season, when the flies retreat from the savannah to the river valleys. In that way large areas can be made fly-free by spraying only a small part, usually in the order of 10 % (discriminative spraying).

So far about 200 000 km^2 have been rendered fly-free by ground spray teams with knapsack sprayers using DDT and dieldrin. This area is about one-fifth of the country and is slightly larger than the area bordering the Sahara desert which is naturally fly-free, but which is only suitable for grazing in the wet season (Davies, 1977). Since 1970 helicopters have been used for aerial residual control, adding another 10 000 km^2 to the reclaimed area, using mainly dieldrin and endosulfan (Spielberger, Na'isa & Abdurrahim, 1977).

Trials with repeated aerosol applications, which had proved successful in Botswana (Kendrick & Alsop, 1974), have so far failed to achieve the required degree of tsetse control in Nigeria and will not be discussed here.

From 1969 onward systematic research into the environmental effects of the Nigeria tsetse control operations has been carried out. Initally birds were chosen as the major indicator organisms. This choice was prompted by the following arguments: (1) Effects of insecticides on birds in the temperate regions were already fairly well described; (2) Birds were known casualties of tsetse ground spray operations (Graham, 1964; Koeman & Pennings, 1970); (3) Birds are well known as a taxonomic group and can be recognized relatively easily, even by people without prior knowledge of the African avifauna. General observations were extended to other vertebrate groups and more recently invertebrate animals have been included in the environmental monitoring programmes.

The work in birds included searches for victims after spraying with subsequent analysis of tissue residues to obtain proof of poisoning, and bird censuses to detect possible changes in species abundance following the application of insecticides. Table 1 gives information on the type of control operations studied.

Both ground and aerial residual application of the organochlorine insecticides used, DDT, dieldrin and endosulfan, caused substantial mortality in a number of bird species, notably insectivorous ones, Other vertebrate groups were affected as well. The mortality pattern differed between application methods and between insecticides, with

Table 1: Tsetse control operations under discussion

Year of spraying	ground/ aerial	insecticide and dose rate (g a.i./ha)		vegetation zone
1969	g	dieldrin	700	Sudan savannah
1975	a*	dieldrin	800	Northern guinea savannah
		endosulfan	800	
1976	g*	endosulfan	1 000	Southern guinea savannah
		DDT	1 000	
1977/78	a*	permethrin	200—300	Northern guinea savannah
		cypermethrin	100—150	
		decamethrin	20— 40	

* experimental spray programmes

aerial spraying affecting a wider range of species. In aerial spraying endosulfan appeared to cause mortality mainly through direct contact, whereas dieldrin appeared to act through the food chain. Koeman et al. (1975) relate this to the faster biodegradability of endosulfan. Residue analysis confirmed insecticidal poisoning as the actual cause of death, but residues in birds netted one year after ground spraying were very low and were considered not to be of toxicological significance (Koeman et al., 1971).

Individual species abundance was assessed by comparison of prominence values (arithmetic mean numbers of birds observed, weighted for frequency of observation (Beals, 1960), calculated over periods before and after spraying. The calculation of prominence values was restricted to those species which occurred regularly throughout the experimental area and which did not flock and were not clearly migratory. The number of species amounted to about one third of the total number in the area.

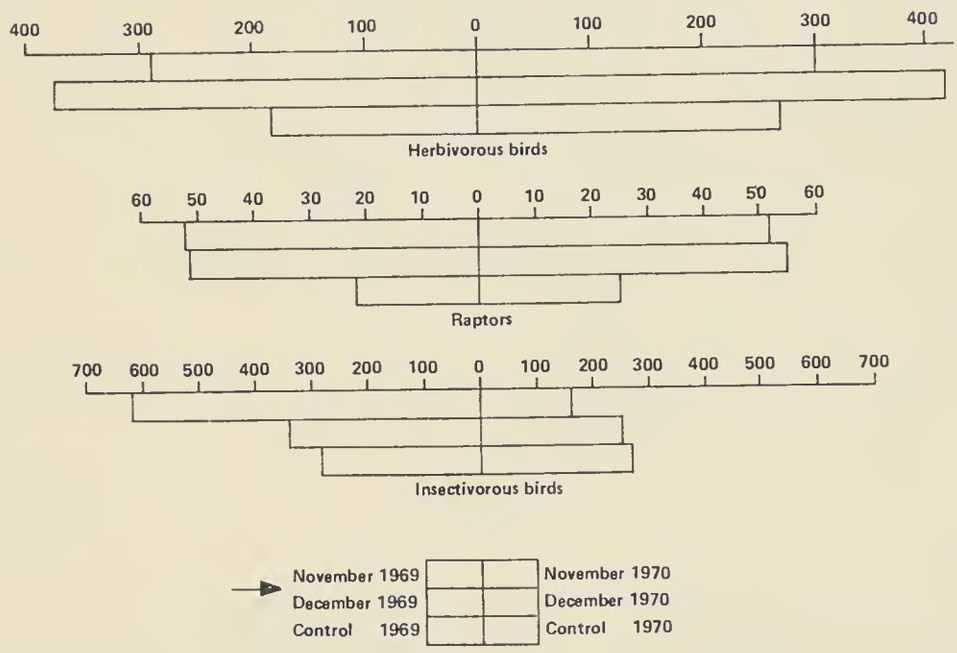

Figure 1. Prominences for trophic groups before and after ground spraying of dieldrin. (Koeman et al., 1971)

Prominence values for birds in different trophic groups were summed and these combined prominences were compared. The data from 1969—1970 show that there were no significant changes in the prominences of herbivorous birds and birds of prey after spraying, but that the prominence of insectivorous birds declined markedly (Fig. 1). Within the insectivorous group some species held their own, but others declined more or less markedly and some disappeared. A similar picture, although less clear-cut, emerges from the data on aerial spraying; with both the insecticides involved a number of individual species showed a decreased abundance (Fig. 2).

Koeman et al. (1971, 1978) point out that within the group of victim species typical fringing forest birds are dominant and that it is precisely these species which show an appreciable decline in prominence after spraying. Since these species are restricted to the riverine forest in their distribution, reoccupation may be difficult, especially if large areas are reclaimed within a short period of time.

In 1977 and 1978 field trials were carried out in Nigeria to test three synthetic pyrethroids for tsetse control. These compounds combine a high insecticidal activity with

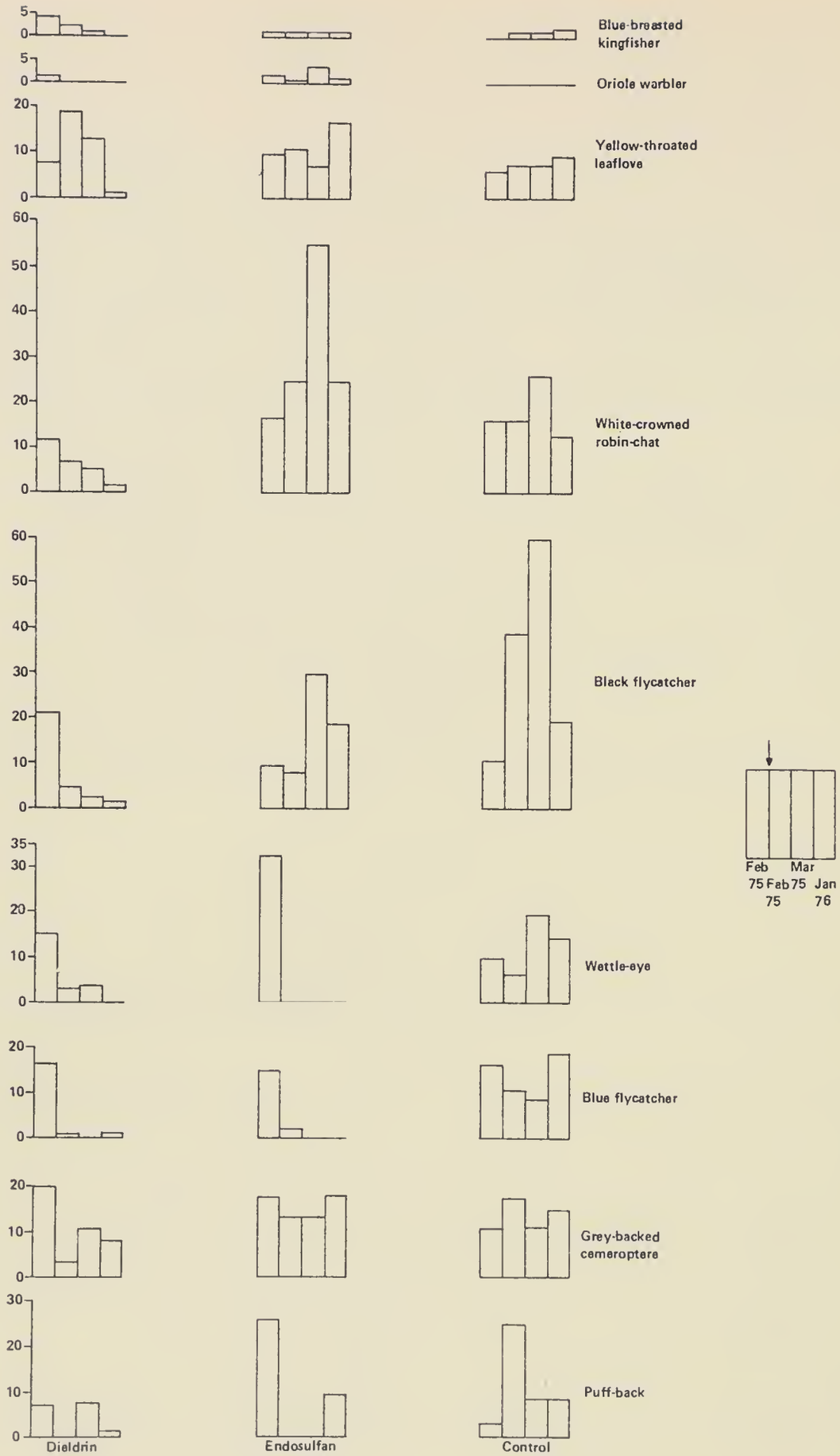

FIGURE 2. Prominence values for insectivorous species before and after aerial spraying of dieldrin and endosulfan. (KOEMAN et al., 1978)

low oral mammalian and avian toxicity and with a good physico-chemical persistence. After spraying no dead birds, nor other vertebrates were found and no marked changes in bird species abundance were noted (Fig. 3). However, mortality was observed among aquatic arthropods, notably shrimps and insects.

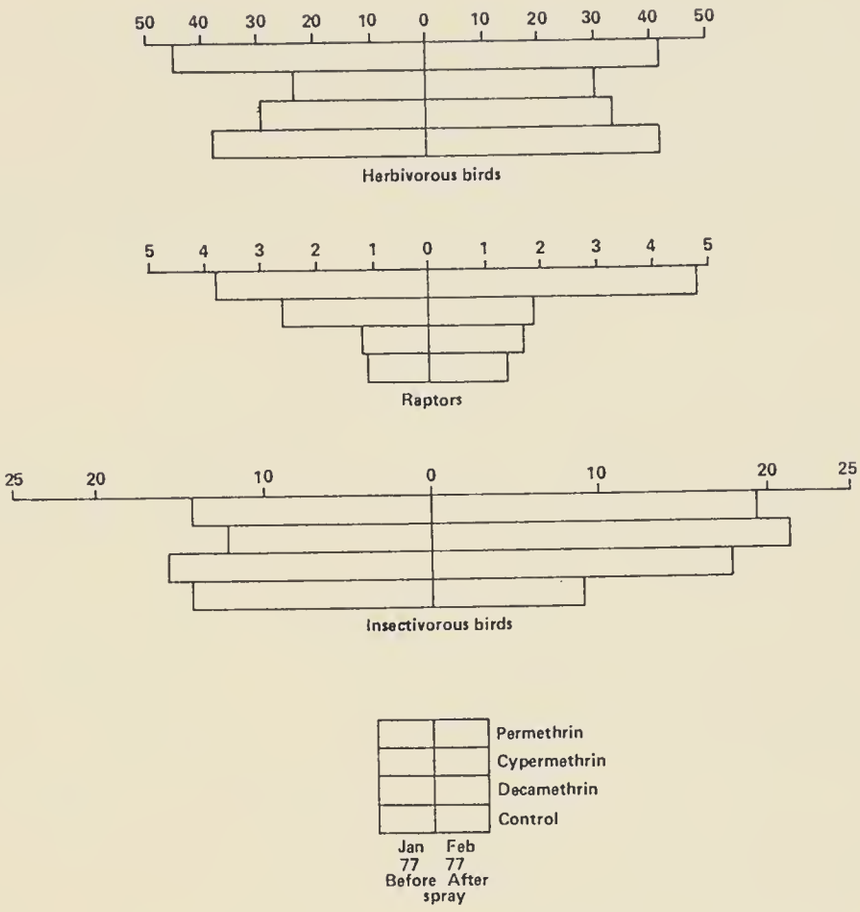

FIGURE 3. Mean number of birds for trophic groups before and after aerial application of three pyrethroid insecticides. (SMIES et al., unpublished)

Conclusion

The results of environmental impact research show that there are differences in the environmental effects between different insecticides and different application techniques. This has been highlighted with the data on birds; for other taxonomic groups the results show analogous but different patterns, albeit less well documented at present. The findings are of interest in themselves, as they give us some insight into the effects of man's actions on the African environment, very necessary in view of the magnitude of the tsetse problem.

At present, insecticides are essential at some stage during an effective tsetse fly control operation. Very few insecticides and application methods give reliable results and in any particular project certain methods may not be practicable.

We hope that environmental impact assessment will be of value in choosing the control methods employed in tsetse control programmes. The need to conserve natural resources can be assessed alongside the factors of feasibility and cost-effectiveness. This should lead to the development of the integrated use of appropriate methodologies in different areas.

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Eggshell Thinning and Organochlorine Residues in the Bat and Aplomado Falcons in Mexico

Lloyd F. Kiff and David B. Peakall

Although DDE-induced eggshell thinning has been demonstrated in western Europe and North America for several falcons, there have been few investigations of this phenomenon in less developed countries, especially in tropical regions where DDT has been used intensively for mosquito control and agricultural purposes. We report here the occurrence of significant eggshell thinning in Mexican populations of the Bat Falcon *Falco rufigularis* and Aplomado Falcon *F. femoralis*, and show a strong negative correlation between the degree of thinning and DDE residue levels in the eggs.

Material and methods

Thickness indices (shell weight in mg/length × breadth in mm, Ratcliffe, 1967) were obtained for whole empty eggshells of Bat and Aplomado Falcons in the collections of the Western Foundation of Vertebrate Zoology, United States National Museum, and the British Museum. The pre-DDT (1897—1941) Bat Falcon sample was collected in the Mexican states of Tamaulipas and Sonora, and the post-DDT sample (1954—1967) was taken in Tamaulipas, Veracruz, and Oaxaca. Pre-DDT (1892—1928) Aplomado Falcon eggshells were from Tamaulipas and the lower Rio Grande Valley in Texas, whereas all post-DDT (1957—1966) eggshells were from Veracruz. Nearly all of the recent specimens of both species were collected by the late Dr. Travis C. Meitzen of Refugio, Texas.

Lipid soluble residues were extracted with hexane from the shell membranes of one or more eggshells from each post-DDT clutch of each species, following the methods of Peakall (1974). The extract was analyzed without clean-up for organochlorine residues by gas-liquid chromatography using an Ni^{63} electron-capture detector. The remaining extract was evaporated to dryness and the weight of lipid determined using a microbalance.

The thickness of eggshell fragments collected from 12 Aplomado Falcon nests in 1977 by one of us (D.P.H.) was measured with a model 35 PS Federal bench comparator thickness gauge and compared to the shell thickness of pre-DDT museum specimens. Ten samples of the 1977 eggshell fragments were immersed in hexane and gently agitated overnight at room temperature to extract the lipid soluble residues.

Results

Bat Falcon

The mean thickness index of Bat Falcon eggshells collected between 1954 and 1967 was 18.0 % less than the thickness index of eggshells taken between 1897 and 1941 (Table 1). The thickest eggshells from the recent sample averaged 6.6 % thinner (set

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TABLE 1: Thickness indices (± standard error) of pre-1947 and recent Mexican Bat Falcon and Aplomado Falcon eggshells

		n*	eggshell thickness index
Bat Falcon	1897—1941	11 (4)	1.28 ± 0.08
	1954—1967	63 (22)	1.05 ± 0.08
	% change		—18.0
Aplomado Falcon	1892—1928	56 (15)	1.50 ± 0.04
	1957—1966	32 (13)	1.12 ± 0.04
	% change		—25.4

* — Number of clutches in parentheses

taken in 1954), and the extreme amount of thinning observed was 28.7 %, occurring in sets collected in 1958 and 1963.

DDE residues were detected in all of the post-DDT Bat Falcon eggshells that were analyzed by gas chromatography. In 35 eggshells collected between 1954 and 1967 DDE residue levels averaged 133 ppm (parts per million of lipid), ranging from

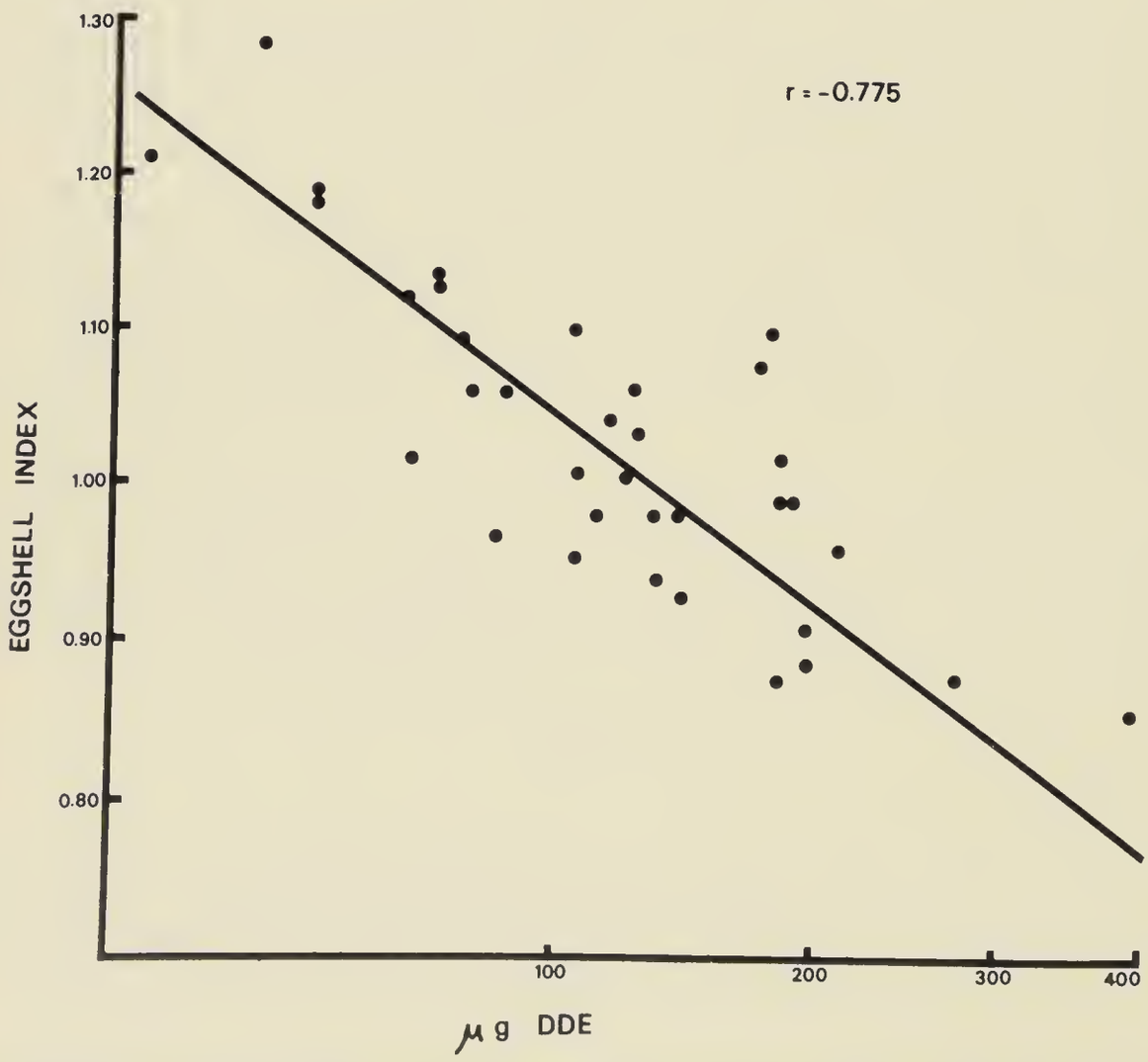

FIGURE 1. Association of DDE residues with Bat Falcon eggshell index (shell weight in mg/length × breadth in mm).

10—400 ppm; DDT residue levels in the same sample averaged 36 ppm (range 5—240 ppm; not detected in two eggs). There was a strong negative correlation between eggshell thickness and DDE level (r = —0.775) (Fig. 1). An approximation of the levels in the entire egg on a wet weight basis can be obtained by dividing the membrane lipid level by twenty.

Six eggshells were subjected to more detailed analyses for organochlorine residues, and unquantifiable traces of polychlorinated biphenyls (1012 and 1242) were found in three, > 50 ppm of dieldrin in three, and 120 ppm of α and γ chlordane in four.

Aplomado Falcon

Eggshells collected between 1957 and 1966 had a mean thickness index 25.4 % less than the average index for eggs taken between 1894 and 1928 (Table 1), ranging from 17.4 % less (set taken in 1964) to 32.7 % less (set taken in 1966).

As for the Bat Falcon, DDE residues were found in all recent Aplomado Falcon eggshells that were subjected to gas chromatographic analyses. DDE residue levels in 20 eggshells collected between 1957 and 1966 averaged 297 ppm (range 110—530 ppm), and the correlation coefficient of thickness index against DDE levels was —0.65. DDT residue levels for the same sample averaged 93 ppm (range 10—210 ppm). In four eggs analyzed in more detail for organochlorine residues, low levels of polychlorinated biphenyls (1012 and 1242) were detected in two, dieldrin in two, and α and γ chlordane in four.

Significant levels of DDE residues were detected in eight of 10 samples of 1977 Aplomado Falcon eggshell fragments. Virtually no lipid could be extracted from the other three samples, so it is to be expected that lipidophilic contaminants would not be detected. In the seven samples that contained at least 0.20 mg of lipid, the DDE content of the whole eggs was calculated to average 296.8 ppm, ranging from 31.0—1280 ppm. Shell thickness of the fragments in these seven samples averaged 0.212 mm, or 24.0 % thinner than the mean thickness of 0.279 mm for 20 Aplomado Falcon eggshells from 20 pre-DDT (1892—1928) clutches.

Discussion

The degree of thinning and the levels of DDE residues found in recent eggs of Mexican Bat and Aplomado Falcons are similar to those documented for north temperate *Falco* populations that have suffered marked population declines (Ratcliffe, 1970; Peakall, 1975). The average decrease in eggshell thickness index in 1954—1967 Aplomado Falcon eggs (25.4 %) and in actual thickness of 1977 eggshell fragments (24.0 %) is particularly severe and is equivalent to the maximum amount of thinning reported for any population of the widespread Peregrine (Peakall & Kiff, 1979). DDE residue levels found in both Bat and Aplomado Falcon eggs exceed those associated with 20 % thinning in Peregrine eggs (Peakall, 1976).

Thinning of over 20 % is likely to result in reproductive failure, primarily from egg breakage (Stickel, 1975). T. C. Meitzen (pers. comm.) stated that several Bat Falcon and Aplomado Falcon eggs that he collected in the late 1950s and early 1960s were so thin-shelled that they could not be prepared by conventional techniques. In 1977 two Veracruz Aplomado Falcon nests contained eggs that were apparently crushed during

incubation. Eggshell thickness at these nests averaged 0.197 and 0.227 mm, or 29.4 % and 18.6 % thinner than pre-DDT eggshells, respectively. At the former nest, a replacement clutch was laid. When the second clutch was inspected shortly after completion, one egg was already dented, and it was crushed during the next two days. Fragments of two eggs of the second set averaged 0.198 mm thick, almost identical to the shell thickness of the first clutch.

The logarithmic relationship between thickness index and DDE residue levels found in Bat and Aplomado Falcon eggs is like the Peregrine (Peakall et al., 1975).

In Europe and temperate North America eggshell thinning has been most severe in bird- and fish-eating species (Anderson & Hickey, 1972; Cooke, 1973). Small birds account for the majority of the biomass in the diets of both Aplomado and Bat Falcons in Mexico, although both species feed regularly on insects and the Bat Falcon also on bats (Hector, unpublished data; J. Szabo, pers. comm.). Meitzen gathered the remains of several Boat-tailed Grackles *Quiscalus mexicanus* and Mourning Doves *Zenaida macroura* at an Aplomado Falcon nest site that contained eggs over 20 % thinner than normal.

Despite legislation restricting the use of DDT in many northern hemisphere countries, it is evident from these data that serious DDT pollution still exists in Mexico. DDE residue levels were virtually identical in the 1957—1966 and 1977 Aplomado Falcon eggshell samples. It is reasonable to assume that this situation is typical for many species in tropical countries where DDT is still widely used.

Acknowledgements

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SYMPOSIUM ON TROPICAL ECOLOGY

10. VI. 1978

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Causes of Tropical Species Diversity

John Terborgh

Introduction

The causes of the high avian species diversity characteristic of humid tropical ecosystems are still an unresolved issue. Numerous suggestions have been advanced, e.g., greater climatic stability and evolutionary age of habitats (Sanders, 1968), more finely subdivided niches (Klopfer & MacArthur, 1961), greater species turnover between habitats (MacArthur, 1969), greater structural complexity of the habitat (MacArthur et al., 1966), higher rates of speciation in tropical regions (MacArthur, 1969; Diamond, 1973; Haffer, 1969, 1974), presence of guilds that are poorly represented or missing in temperate communities (Orians, 1969; Karr, 1971), and broader tropical resource spectra (Schoener, 1971), but few of these suggestions have been adequately investigated independently of the others.

Here I proceed in a pragmatic way to categorize the "extra" species found in a tropical forest when a temperate forest community is taken as a frame of reference. The additional tropical species are attributed to both ecological and evolutionary differences between the two sites.

Methods

I examine two bird communities, one inhabiting a mature warm temperate forest, the other, a plot of lowland moist forest in the Amazon basin. The breeding species of the two forests are assigned to a set of 24 trophic/behavioural guilds that effect a rough two-dimensional functional ordination of the communities on axes of diet and foraging tactics. A third dimension is then included by comparing the weight ranges of the species representing each guild in the two forests. Classification of the species into guilds is based largely on personal observation, though in a few cases the assignments rest on reported stomach contents (in Bent [1919—1968] for North American species; Haverschmidt [1968] for South American species).

Properties of the study sites

The vegetation of both sites is essentially undisturbed. A 5,000 ha tract of flood plain forest along the Congaree River in central South Carolina (latitude 33°) constitutes the temperate site. It has a multi-layered architecture that includes more than 35 species of trees, among which *Liquidambar, Fraxinus, Quercus* and Ulmaceae predominate. Canopy trees average 35 m in height, though occasional crowns rise to 45 m. The internal structure consists of one or two sub-canopy tree layers, palmetto *(Sabal)*, bamboo *(Arundinaria)* and herbs on the ground, many climbing vines and lianes *(Campsis, Vitis)* and a moderate development of vascular epiphytes *(Tillandsia, Polypodium)*. In its stature, stratification, tree species diversity, variety of growth forms and general luxuriance, this forest equals or surpasses many tropical forests.

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TABLE 1: Guild Structure, Guild Niche Breadth and Species Packing in the Bird Communities of a Tropical and Temperate Forest and apportioning of the additional species

	Tropical Forest				Temperate Forest				Additional tropical species due to		
Guild	No. species	Weight (g) min—max[1]	Included niche[2]	Packing[3]	No. species	Weight (g) min—max	Included niche	Packing	Guild not represented in temperate forest	Larger tropical niche[5]	Increased species packing[6]
Carrion	2	1,600—3,125	1.0	1.0	1	2,100	—	—		1	0
Raptor											
general (mammals, etc.)	7	380—4,250	3.5	1.7	1	1,020	—	—		3	3
bird	4	100—540	2.4	1.2	1	470	—	—		2	1
other (snails, reptiles, insects)	7	160—610	1.9	3.1	1	280	—	—		2	4
Owl	5	65—760	3.5	1.1	2	165—780	2.2	0.4		0	3
Nightjar[4]	1	40	—	—					1		
Mast eater											
terrestrial	5	210—1,010	2.3	1.8	2	142—6,100	5.42	0.2		0	3
arboreal	8	170—1,150	2.8	2.5					8		
Frugivore											
terrestrial	3	100—3,400	5.1	0.4					3		
arboreal	18	9—1,500	7.4	2.3	1	130	—	—		7	10
Nectarivore	8	3—8.5	1.5	4.7	1	4	—	—		1	6
Insectivore											
terrestrial	10	11—55	2.3	3.9	2	20—49	1.3	0.8		1	7
woodpecker	8	10—220	4.5	1.6	5	25—260	3.4	1.2		1	2
bark gleaning	9	13—135	3.4	2.4	1	22	—	—		3	5
foliage gleaning	19	9—105	3.5	5.1	15	6—75	3.6	3.8		0	4

TABLE 1: (continued)

Guild	Tropical Forest				Temperate Forest				Additional tropical species due to		
	No. species	Weight (g) min—max[1]	Included niche[2]	Packing[3]	No. species	Weight (g) min—max	Included niche	Packing	Guild not represented in temperate forest	Larger tropical niche[5]	Increased species packing[6]
sallying	27	4.5—108	4.6	5.7	3	12—34	1.5	1.3		4	20
aerial	4	10—50	2.3	1.3	1	25	—	—		2	1
ant following	6	19—70	1.9	2.7					6		
dead leaf gleaning	7	10—63	2.7	2.3					7		
vine gleaning	7	7—85	3.6	1.7					7		
Frugivore/predator	6	130—540	2.1	2.4	2	87—350	2.0	0.5		0	4
Frugivore/insectivore											
arboreal, gleaning	12	14—52	1.9	5.8	1	44	—	—		2	9
arboreal, sallying	13	11—85	3.0	4.1					13		
Frugivore/insectivore/ nectarivore	11	11—360	5.0	2.0					11		
Total	207				40				56	29	82
Percent of additional tropical species									34	17	49

[1] Weights of the smallest and largest guild members.

[2] Computed as $\log_2 \frac{\max}{\min}$, where min and max refer, respectively, to the weights of the smallest and largest guild members. See text for details.

[3] Species packing computed as the number of species in the guild $-1 \div$ the included niche. See text for details.

[4] Guilds in bold type are found in the tropical forest but are evidently lacking in the temperate forest.

[5] (Tropical included niche) $\times$ (temperate species packing in that guild) = (no. of species that would be in the tropical guild at the temperate packing value -1). (This $+1$) $-$ (no. of species in the temperate guild) = (extra species attributable to a broader tropical guild niche). Packing in temperate singleton guilds was assumed = 1.0.

[6] (Total of extra species in the tropical guild) $-$ (no. of extra species due to broader tropical niche) = (extra species due to increased tropical packing).

The tropical site was a typical tract of Amazonian terra firme forest, located at 9° 35′ S and 74° 55′ W in Biological Station Panguana of Prof. H. W. Koepcke. Although occasional emergent crowns reached 50 or 55 m *(Ceiba, Dipteryx)*, the average stature of canopy trees was less than in the South Carolina forest (ca. 30 m). The internal structure was more complex, however, with more foliage at low and middle levels, more tree layers, and greater numbers of tree species, palms and lianes.

Results

The avian community of the tropical forest included 207 species, while that of the temperate forest included only 40 species, a difference of more than 5-fold. My objective is to account for this difference as it relates to the functional roles of individual species in their respective communities. The first step is to classify each species into one of 24 trophic/behavioural guilds (Table 1). The tropical community differs from its temperate counterpart in having more guilds, more species per guild, somewhat broader guild niches (as defined by the weight ratio of the largest and smallest species) and tighter species packing within guilds.

Computation of included niches and species packing

Any guild represented in both communities may contain different numbers of species with different minimum and maximum weights. These contrasts are readily resolved into two components, one related to the functional dimension of the niche space occupied by the guild (included niche), and the other related to the density of species that are arrayed along the niche dimension (species packing).

Species which are closely related ecologically, and which differ functionally mainly in size, often differ by a factor of 1.2—1.3 in length or by a factor of roughly 2 in weight (Hutchinson, 1959; Schoener, 1965, 1970; Diamond, 1973). Following this rule, I define the weight dimension of the guild niche as $\log_2\left(\frac{\max}{\min}\right)$, where max and min are the weights in grams of the largest and smallest guild members. This gives the number of doublings in size that separate the two extreme guild members, and, by inference, a representation of the niche space being exploited by the guild.

A measure of species packing is now easily obtained by dividing the number of species in the guild minus one by the included niche. The quotient expresses the number of guild members per doubling in size within the guild niche.

Apportioning the extra tropical diversity

We may now apportion the extra species present in the tropical forest into three distinct categories: (1) members of guilds that are not represented in the temperate forest (34 %), (2) species whose presence may be attributed to broader tropical guild niches (17 %) and (3) species whose presence may be attributed to tighter packing within tropical guilds (49 %). The first category implies the existence of several qualitatively distinct additional niches in the tropical forest, the second implies quantitatively broader niches and the third implies that tropical species are more tightly packed within their guilds, or any of a number of other possibilities to be mentioned later.

Additional niches

Two clear-cut examples are obligate ant followers and obligate dead leaf gleaners. Neither army ants nor quantities of suspended dead leaves occur in the temperate forest, thus opportunities for the respective modes of life simply do not exist. Much the same can be said of frugivory. Most of the soft fruit produced by the temperate forest drops in the fall and winter. During the nesting season there is essentially none available. Vine gleaning is a less clear-cut case. Several of the temperate foliage gleaners forage facultatively in vines, but none of them does to the extent realized by members of the tropical guild. Mixed foraging habits are not well represented in the temperate community, primarily because of a scarcity of soft fruits and nectar sources during the summer months. Finally, several tropical raptors included in the "Other" guild pursue specializations not represented in the temperate community, e.g., feeding on hymenoptera, snails, reptiles.

Breadth of niche

For guilds containing two or more species in both communities, there is no consistent pattern in the relative size of the included niches. In three cases the temperate niches are larger, in two cases the tropical niches are larger, and in two cases the niche breadths are approximately equal. This suggests that the underlying resource spectra are not systematically broader in the tropical forest, although there may be a slight tendency for the largest species in tropical guilds to exceed their temperate counterparts.

A majority (9/16) of the temperate guilds contain only one species, while this is true of only one of the tropical guilds. It seems remarkable that each of the temperate singleton guilds consists of a species whose weight falls nearly in the middle of the range circumscribed by its tropical counterparts, a fact that may indicate convergence in the underlying resource spectra. The reduced number of species in the temperate guilds could be due to ecological factors, i.e., narrower resource spectra with modal values similar to tropical counterparts, or to evolutionary factors, i.e., reduced numbers of guild members present in the local fauna. In the latter situation a greater versatility in diet and behaviour would be predicted for temperate species. Both possibilities are amenable to test. The procedure followed here apportions extra tropical species more or less evenly to the two causes.

Species packing

The category of extra species attributed to tighter tropical species packing, as I have operationally defined it here, is really a catch-all. It includes all modes of ecological segregation that are not included in the guild and weight ordinations, the effects of differences between the two forests in their structure, productivity, resource spectra (in part), and seasonality, as well as real increases in species packing.

A notable feature of the results is that guilds differ strikingly in their apparent levels of species packing. Guilds that exploit structurally simple niches such as open airspace (aerial insectivores) or dead wood (woodpeckers) and ones dependent on narrowly defined diets that require special adaptations (vultures, bird hawks), show low packing values (≤ 1.6) in both communities, implying that the ways for subdividing these niches are limited. Owls also show low packing, but the reason for this is less evident.

Even among guilds exploiting two-dimensional substrates there appear to be possibilities for specialization. Terrestrial insectivores, for example, may pick exposed prey from the surface of the leaf litter, or turn the litter over to reveal hidden prey, or search the dark recesses of fallen logs and brush piles, or, in one case, flutter up to capture insects from the undersurface of low foliage. Among the bark gleaners, there are species which simply pick prey from the surface, others that flake away loose bark, others that probe into cavities or epiphytes and still others that sally out from trunks to capture flying insects.

At the extreme are some guilds in which the packing levels are very high (> 3.5). All of these are arboreal (sallying and gleaning insectivores and mixed frugivore-insectivores, nectarivores), and exhibit pronounced vertical stratification (Terborgh, 1980). Clearly more opportunities for specialization are available within foraging modes that permit three-dimensional, vs. one or two-dimensional, use of the habitat.

It is apparent that in the tropical forest major functional roles are more finely subdivided. In some instances the differences are inadequately exposed by the procedure I have followed. Table 1 indicates, for example, that the two forests harbor similar numbers of arboreal foliage gleaners (15 temperate vs. 19 tropical). This grossly underestimates the real difference. The function performed by the seven vine gleaning specialists in Peru is included in the repertoires of some of the 15 South Carolina foliage gleaners. Many of the 27 tropical salliers feed on stationary prey snatched from the surfaces of leaves. This is really a specialized gleaning function that enables capture of quick, mobile prey. And in addition, the Peruvian forest contains 36 partially insectivorous mixed feeders vs. one in South Carolina. Thus the contrast between the two situations is indeed very great, even if it is only crudely represented by my analysis.

Causes of increased tropical species packing

Extra tropical diversity attributed to increased species packing represents a component of diversity that is not accounted for by differences in available resources or in the character of the habitat. To what can it be attributed? In my opinion it is due to an historically greater rate of speciation, perhaps coupled with lower rates of extinction, producing a higher regional species density. Although similar views have been repeatedly expressed in the literature (e.g., Darlington, 1957; MacArthur, 1969; Diamond, 1973; Terborgh, 1973), no previous attempt has been made to specify the fraction of tropical diversity that is a consequence of evolutionary, as opposed to ecological differences between temperate and tropical regions.

High rates of speciation are clearly implied by Haffer's (1969) work. Recurrent dry periods during the Pleistocene repeatedly subdivided the Amazonian forest into a dozen or so isolated refugia, providing abundant opportunities for geographical isolation. Wet periods, alternating with dry ones, presumably allowed the forest to coalesce into single interconnected units resembling the present one, providing opportunities for secondary contact, character divergence and faunal equilibration. Repetition of these cycles led to a remarkable proliferation of species in many Amazonian genera (Haffer, 1974; Fitzpatrick, 1976).

As a consequence of the symmetrical location of Amazonia astride the equator, climatically similar forest refugia could occur in all corners of the region: north, south,

east and west. In contrast, the North American fauna was able to retreat from the climatic deterioration in only one direction—southward, and had available to it only two possible refugia, the Florida peninsula and Mexico. Thus, the likelihood of extinctions in North America was probably greater, while the potential for speciation was a great deal less.

Acknowledgements

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Structural Complexity and Species Clustering of Birds in Tropical Rainforests

Jiro Kikkawa, Thomas E. Lovejoy and Philip S. Humphrey

Recent advances in ordination techniques permit analysis of complex associations of many species of birds with a large number of environmental attributes found in tropical rainforests (Webb et al., 1973). In this paper we present the results of an analyses of such associations at two localities in the Amazon Basin.

Data collection

1. The Guamá Ecological Research Area, Belém (1°26' S, 48°29' W), Lower Amazon, Brazil. The area contains: (1) "terra firme" forest on dry ground with its secondary growth ("capoeira"), (2) "varzea", a riverine swamp forest subject to tidally induced flooding twice daily, and (3) "igapó", a permanent swamp forest (Lovejoy, 1975). Data were obtained from 100 groups of mist-nets: low-net groups of three 12 m mist-nets (70 groups) and four mist-nets of 12 m and 6 m (6 groups) and high-net groups of three 12 m nets (23 groups) and four 6 m nets (1 group) forming a wall under the canopy. No birds were removed from the study area except for a few netting casualties. Three low-net groups and six high-net groups caught no birds; the rest caught 666 individuals of 74 species in 17 days in 1971.

2. Santa Cecilia (0°02' N, 76°58' W), Napo Province, Upper Amazon, Ecuador. Three 12 m mist-nets were placed on three sides of each of thirty sites selected in the terra firme forest and were operated for 15 mornings between 29 June and 15 August 1971. No high-nets were used. Most netted birds were collected; only the species frequently captured were released, which caused the difference between the total catch (1,203) and the number of individuals in it (973). The latter, representing 124 species, was used in the analysis after combining captures for the three nets at each site.

Environmental information was collected by means of a pro forma survey. The pro forma contains 300 items, each with several states objectively defined by measurements taken within 20 m × 20 m plots. It covers local topographic and edaphic features, physiognomic and structural attributes of vegetation, and flowering, fruiting and defoliating characteristics of plants. At Belém one hundred sites were examined in July—August 1971, immediately following the netting operation. At Santa Cecilia all thirty sites were surveyed in June—July 1971 at the beginning of the netting operation.

Data processing

The pro forma data were simplified by limiting attributes to those that showed significant variation among sites and reducing the number of states to binary or up to four grades. The data for the heights of canopy and emergents, and for Santa Cecilia the elevation, were used without scaling. This preliminary treatment of the field data

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produced 58 qualitative (binary), 72 numerical (scoring) and 13 disordered multistate attributes, a total of 143, for the Belém sites and similarly 62, 55 and 14, respectively, giving a total of 131 attributes, for the Santa Cecilia sites.

The study sites were ordinated by means of the principal coordinate analysis (program GOWER), using the bird data for one set and the environmental data for another. For calculating the intersite dissimilarity the Canberra metric was used for the Belém data and the Bray-Curtis measure, which gave more weight to the frequency of captures than the mere presence of species, was used for the Santa Cecilia data. The two sets of orthogonal Gower vectors were then subjected to canonical analysis (program CANONGO) and the resultant canonical vectors were back-correlated with the original bird and environmental data. All computer analyses were run on the Cyber 76 at the CSIRO Division of Computing Research in Canberra.

Results

1. Belém. Species diversity of netted birds (H' with log, base e) was 3.66, somewhat lower than obtained for the 1968—69 captures (Lovejoy, 1975). In ordination (Fig. 1) all high-net sites appeared in the same quadrant while the low-net sites gave a wide spread in the bird vectors. The terra firme and varzea sites tended to group together; the igapó sites were scattered widely away from the rest. The environmental vectors showed a gradient between the varzea and terra firme sites, separate from a group of igapó sites. Bird vector 1 had two abundant species with wide habitat tolerance *(Glyphorhynchus spirurus* and *Arremon taciturnus)* at the positive end showing relatively high correlation coefficients and no species at the negative end; bird vector 2 had an abundant, habitat tolerant species *(Myrmotherula hauxwelli)* at the negative end and another abundant species *(Myrmotherula axillaris),* known to have its highest abundance in igapó (Lovejoy, 1975), at the positive end.

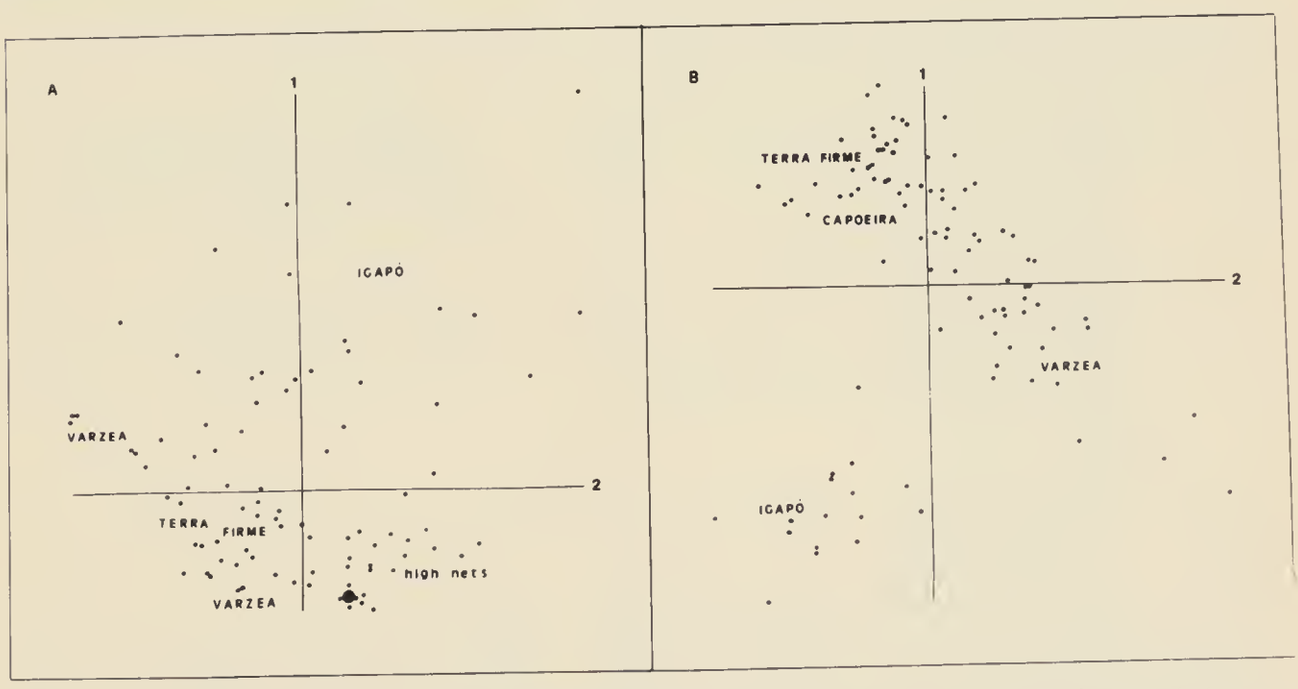

Figure 1. Ordination of 100 net sites at Belém, showing the coordinates of the first and the second vectors based on the bird data (A) and the environmental data (B). Groups of sites representing particular habitat types and a group of high-net sites are indicated. In the bird ordination 9 sites which caught no birds occupy the identical coordinates indicated by a large circle.

In canonical analysis between the bird and environmental vectors (Table 1) only the first canonical vector showed strong site coincidence, particularly of igapó. The result of back-correlation with the original data for the first canonical vector (Table 2) shows the correlation of major original vectors with canonical vectors indicating the importance of association of relatively common species with edaphic and related features such as abundance of palms and holes in the ground.

TABLE 1: Canonical correlations between bird and environmental vectors (Belém)

Canonical vector	I		II		III	
Correlation	0.773		0.619		0.501	
Gower vectors	birds	environment	birds	environment	birds	environment
1	0.812	—0.600	—0.088	—0.689	0.517	0.282
2	0.346	—0.342	—0.552	0.608	—0.713	0.552
3	0.444	0.471	0.678	—0.107	—0.437	0.227
Site coincidences in canonical coordinates	strong, igapó (8 low-net sites) versus T. F. sites		weak, some varzea sites		weak, high-net sites	

2. Santa Cecilia. Although netting was limited to the low layer of the forest (up to about 2.5 m) in about 8 ha of relatively unvaried habitat (28 sites in terra firme rainforest and 2 sites in bamboo thickets) and was operated for a short period, the total num-

TABLE 2. Correlation coefficients between canonical vectors and original data (Belém)

		Vector I	
r	bird species	r	environmental attributes
0.714	*Arremon taciturnus* (Fringillidae)	0.877	small holes in ground, natural
		0.863	soil deep and highly organic
0.633	*Myrmotherula axillaris* (Formicariidae)	0.698	presence of emergents with umbrella-shaped crown
0.615	*Hypocnemoides maculicauda* (Formicariidae)	0.698	high proportions of emergents having laminate leaves
0.611	*Cercomacra tyrannina* (Formicariidae)	0.698	presence of palms among emergents
		0.675	large holes in ground, natural
0.578	*Sclateria naevia* (Formicariidae)		
0.533	*Xenops minutus* (Furnariidae)		
0.525	*Chloroceryle aenea* (Alcedinidae)		
no bird species with high negative correlations		—0.698	high proportions of emergents having irregular crown
		—0.761	emergents with high order of branching
		—0.864	soil deep but not highly organic
		—0.877	small holes in ground, made by animals

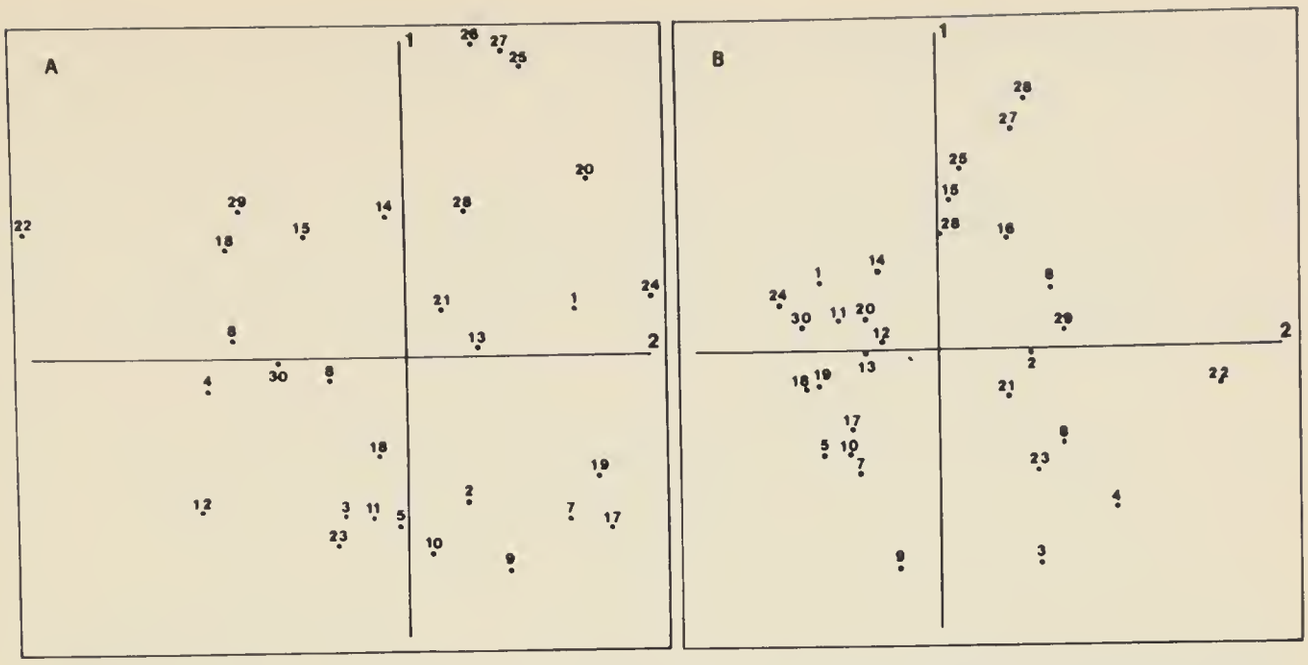

Figure 2. Ordination of 30 net sites at Santa Cecilia, showing the coordinates of the first two vectors based on the bird data (A) and the environmental data (B).

ber of birds caught was extremely high. In a forest habitat of a similar altitude in the upper Amazon Basin of central Peru, Terborgh & Weske (1969) operated low nets at the same time of year and caught 51 species out of a total of 141 known to occur in the forest. If the same ratio were applied to our low-net captures the estimated number of species in the area would be 335. Species diversity (H' with log, base e) of netted birds alone was 4.23 (3.34 if the first 100 birds—40 species—were used for calculation) and the density was on the order of 5,000 birds per 40 ha (100 acres) if elimination of netted birds did not affect the populations significantly. These values represent by far the highest diversity and density of birds ever recorded for land birds. The pattern of captures from one five-day netting period to the next for all nets indicated that most species were resident at the time of netting. Common species tended to occur in most sites while the rarely caught species did not show similar patterns in the sharing of the sites or concentration in particular sites. The number of species caught at a net-site varied from 13 to 38 out of a total of 124.

Table 3: Canonical correlations between bird and other vectors (Santa Cecilia)

Canonical vector	Bird and environmental vectors					
	I		II		III	
Correlation	0.924		0.770		0.677	
Gower vectors	birds	environment	birds	environment	birds	environment
1	0.922	0.780	−0.205	0.533	0.255	−0.248
2	−0.186	0.052	0.175	−0.421	0.479	−0.300
3	0.141	0.279	0.670	−0.158	−0.201	0.527
Site coincidences in canonical coordinates	strong, bamboo sites versus complex forest		strong, bamboo sites versus sites with emergents		weak	

In ordination for the first two vectors (Fig. 2) the bamboo sites tended to be segregated and the rest showed no obvious resemblance among them. The canonical analysis (Table 3) between the bird and environmental vectors produced higher correlations than the one for Belém. The result of back-correlations with the original data for the first canonical vector (Table 4) shows relatively high correlations between the characteristic attributes of the bamboo sites and associated species, particularly frugivores and nectarivores, and rather diffused association of many other bird species with the features of climax rainforest.

TABLE 4: Correlation coefficients between canonical vectors and original bird and environmental data (Santa Cecilia)

		Vector I	
r	bird species	r	environmental attributes
0.649	*Automolus dorsalis* (Furnariidae)	0.775	basal features of trees, cylindrical
0.643	*Manacus manacus* (Pipridae)	0.724	bark below 8 m, high proportions totally exposed
0.595	*Teleonema filicauda* (Pipridae)	0.713	presence of smooth bark
0.573	*Pipromorpha oleaginea* (Tyrannidae)	0.708	height of ground layer greater than 1 m
0.540	*Hypocnemis cantator* (Formicariidae)	0.685	vines abundant in ground cover
0.526	*Threnetes leucurus* (Trochilidae)	0.552	dead stems abundant
0.510	*Phaethornis hispidus* (Trochilidae)	—0.612	robust woody lianes common
0.506	*Automolus rufipileatus* (Furnariidae)	—0.614	plank buttresses common
—0.456	*Myrmotherula hauxwelli* (Formicariidae)	—0.634	high proportions of trees non-buttressed
		—0.644	palms in tall-shrub layer
		—0.711	high proportions of tall shrubs having laminate leaves
		—0.711	high proportions of tall shrubs having irregular crown shape
		—0.721	severe degrees of damage to foliage above 8 m by insects und fungi
		—0.736	some trees defoliated
		—0.737	large clumps of epiphytes above 8 m common
		—0.795	emergents with high order of branching
		—0.807	foliage of tree layer dense
		—0.815	bark below 8 m mostly finely textured

Discussion

We selected two study areas in the region of the greatest species diversity of birds—the Napo and the Para refugia (MÜLLER, 1973; HAFFER, 1974). These areas contain specially large numbers of lower strata forest birds with restricted ranges of movement (LOVEJOY, 1975; PEARSON, 1975). In our results relatively rare birds revealed only marginal association with particular components of the habitat; common species with great niche width tended to discriminate more regularly than the rare species between certain habitat components. These components included edaphic conditions and foliage densi-

ties of the low and uppermost strata of the forest. The results did not suggest segregation among the species. Instead, species belonging to the same foraging guild tended to cluster along the major canonical vectors, suggesting their association with particular habitat components.

Much clearer patterns should have emerged on the basis of the relation between bird species composition and tree species composition demonstrated with overlap measures for Belém forests (Lovejoy, 1975) and on the basis of E. J. Williams' analysis of the same data (Humphrey & Hatheway, in MS). That they were not obtained is most likely a consequence of the small bird data base used in the analyses.

To what extent such patterns will be revealed by a larger data base depends on (1) how faithful the birds are to the components of the habitat measured and (2) how frequently they appear where the associated components exist. For example, bird species are not as sensitive as tree species in responding to the soil moisture gradient (Lovejoy, 1975). Even if the answer to the first question is favourable to the demonstration of associated patterns, many rare species may still have patchy distribution and may not utilise their habitat fully. This would mean that the data base necessary for producing predictive models will accumulate slowly.

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Why are Many Tropical Bird Species Distributed Patchily with Respect to Available Habitat?

Jared M. Diamond

Introduction

The title of this paper may enrage ornithologists from the temperate zones. After all, an accepted test of being a "good bird-watcher" in the temperate zones is the ability to predict, just by looking at a piece of habitat, what bird species will be found there. Two tacit assumptions underlie this test: 1. presence or absence of most bird species is deterministically linked to habitat properties; 2. a good bird-watcher can and should learn by experience what habitat properties determine the distribution of each bird species. Hence, if a temperate-zone bird-watcher asserts that a bird species is missing from a suitable piece of habitat, one can more often infer an incompetent bird-watcher than an interesting ecological problem.

This test does not work in the tropics, especially in species-rich areas such as New Guinea, the neotropics, Africa, southeast Asia, and Sundaland. Many tropical bird species really are patchily distributed with respect to suitable habitat: they may even have patchy distributions in a continuous expanse of habitat. (I shall not discuss species that are patchily distributed merely because their habitat itself is patchily distributed and the species fills all available habitat patches). After presenting examples involving New Guinea birds, I shall suggest possible explanations.

Evidence for patchy distributions in New Guinea

Ornithological exploration of New Guinea began in 1818. Since 1860 most areas of the island have been surveyed repeatedly. In recent decades much further information has been obtained from New Guinea village people, many of whom are walking encyclopedias of bird lore. These accumulated records show that, on a geographical scale, the distributions of many species are patchy within a continuous expanse of suitable habitat, and that many of the patches have retained their gross positions for over a century (Diamond, 1972, 1973, 1975). Consider some examples:

The Central Mountain Range of New Guinea extends from east to west for 1,000 miles, with elevations up to 16,500 ft and no passes under 5,000 ft. Most of New Guinea's ca. 180 montane bird species extend to both the west and east ends of the Range. Nevertheless, each portion of the Range lacks some otherwise widespread old species. For example (Fig. 1), the tree creeper *Climacteris leucophaea* is encountered daily in the mountains of east and west New Guinea, where it is common, has a loud song, and occupies a broad altitudinal range (4,500—10,000 ft) including several forest types. This species has a distributional gap of about 250 miles in the middle of the Central Range, although mountains and forests with similar bark and tree species extend uninterrupted for 1,000 miles, and although there is no other New Guinea species that is in the same family or ecologically close. Numerous expeditions and resident obser-

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vers have explored this area since 1951, and New Guinea villagers who have spent their lives in this area and then have become familiar with *Climacteris leucophaea* in east New Guinea are positive that it does not occur in this area.

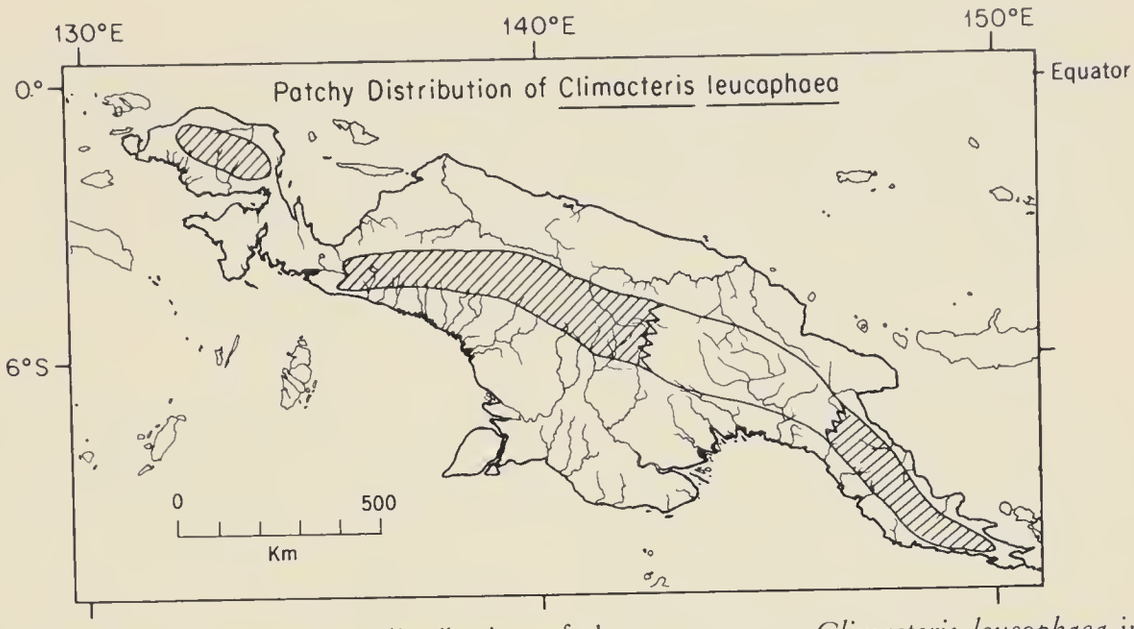

FIGURE 1. Hatching indicates the distribution of the tree creeper *Climacteris leucophaea* in the mountains of New Guinea. The Central Range is outlined. Note the distributional gap of 250 miles in the middle of the Central Range. (After DIAMOND, 1972.)

Twenty-one other montane species exhibit similar gaps of several hundred miles along the Central Range (DIAMOND, 1972, pp. 17—26). Some of the gaps are in the east, some in the centre, some in the west. Other species have gaps of several hundred

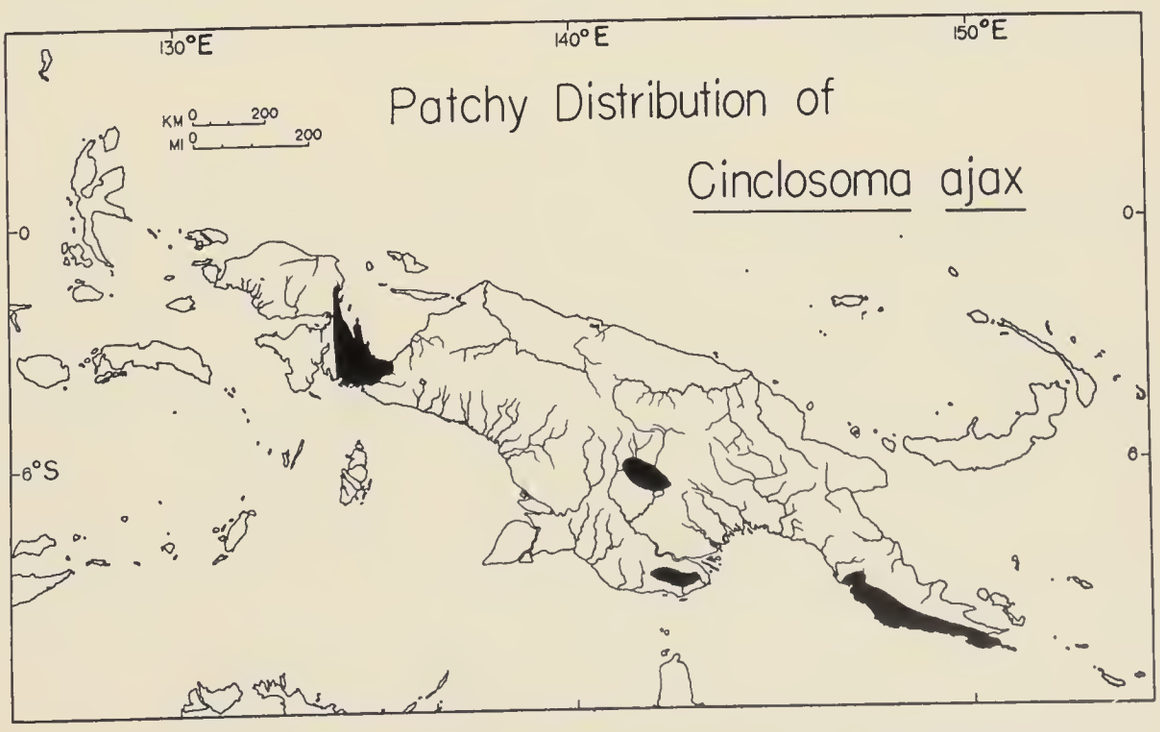

FIGURE 2. Patchy distribution of the logrunner *Cinclosoma ajax* in the lowlands of New Guinea. The species occurs only in four far-flung areas. (From DIAMOND, 1975.)

miles in the hill forests and lowlands, which form a broad ring around the mountain backbone (cf. DIAMOND, 1975, Fig. 36).

These cases involve species with one or two major distributional gaps in an otherwise continuous range. For other species the gaps are much larger and more numerous than the occupied areas, so that the species' range consists of large but scattered patches. For example, the range of the logrunner *Cinclosoma ajax,* the sole New Guinea species of its genus, consists of four large patches in the lowlands (Fig. 2). The berrypecker *Melanocharis arfakiana,* the ultimate in avian patchiness, is known from two localities at opposite ends of New Guinea, 1,000 miles apart (DIAMOND, 1975, Fig. 38).

Some generalizations about patchiness

Any theory of patchiness must explain not only why it is much more marked in the tropics than in the temperate zones, but also why it is much more marked on species-rich than on species-poor tropical islands. In the tropical southwest Pacific patchy distributions are most marked on the four most species-rich islands (New Guinea, New Britain, New Ireland, and Guadalcanal), whereas intensive local surveys record nearly 100 % of the species known from the lowlands of species-poor Pacific islands (DIAMOND, 1979).

Whatever the explanation for patchiness, it is probably significant in speciation. Ornithologists have often wondered how rich avifaunas could evolve in tropical areas presently lacking obvious barriers to bird dispersal. The distributional gaps in a continuous habitat expanse illustrated by Figs. 1 and 2 show that tropical populations can be isolated without obvious geographic barriers, and that one need not always postulate vanished barriers of alien habitat (e.g., non-forest barriers during dry phases of the Pleistocene, as discussed for Amazonia by HAFFER (1974)) to account for the geographic isolation prerequisite to speciation. For example, present-day patchiness affords a ready explanation for speciation in New Guinea's montane avifauna (DIAMOND, 1972, pp. 22—23; 1973, Fig. 8).

Theories of patchiness

I suggest four explanations that may act singly or in combination:

1. "It's really just a patchy habitat, but you didn't discern it and therefore you're a bad bird-watcher"

There are many ecologically well known, patchily distributed species for which conditions in the distributional gap seem well within the range of conditions under which the species lives outside the gap. Nevertheless, sceptics can protest: "You think that the areas where your species is missing are ecologically suitable, but maybe they're not. Tropical birds may have subtle habitat requirements. The gap may be distinguished by some factor important to birds but invisible to you — the absence of some food plant or soil mineral, or the presence of some disease or parasite. More generally, how can you be sure that the gap isn't due to some unspecified ecological factor?"

Of course, one can by definition never rule out the possible existence of unspecified factors. However, many patchily distributed species occupy such a great variety of

habitats and climatic zones in their blocks of occurrence as to make a postulate of undetected habitat requirements implausible. For instance, on islands where the whistler *Pachycephala melanura* is the sole species of its genus, it is abundant in all elevational zones from sea-level to the summits, in a range of habitats from gardens to coconut groves to savanna to rainforest to montane cloud forest to subalpine shrubbery, in all vertical layers from understory to canopy. On New Guinea it is confined to forest between 4,500 and 7,700 ft in one valley, and this confinement surely has more to do with the presence of 14 competing whistler species on New Guinea than with adaptive limitations of this ecologically catholic species. Similarly, the wide range of forested habitats occupied by *Climacteris leucophaea* in west and east New Guinea is matched in vegetational physiognomy as well as in principal plant species by habitats lacking this bird in central New Guinea.

2. Historical effects

An environment that is homogeneous today may have been patchy in the past. If bird distributions respond more slowly to environmental change than does forest structure, present bird distributions may continue to reflect past patches. A clear example is provided by 21 New Guinea species represented by lowland populations in a clear patch near the mouth of the Fly River. If we did not realize that these Fly Mouth forests had been joined to cooler subtropical forests of Australia during the Pleistocene and that these isolated populations are relicts, their occurrence would be a mystery. The numerous neotropical species still confined to the Pleistocene site of the Napo forest refuge provide a similar example for South America. However, practically any area in New Guinea proves to be the site of a patch for some species, so it seems unlikely that all distributional patchiness can be explained in terms of relict population patches from the Pleistocene. We expect present-day bird patchiness resulting from Pleistocene habitat patchiness to be more marked in the tropics than in the temperate zones, as the greater vagility of temperate-zone bird species would more quickly cause such historical effects to disappear.

3. Immigration-extinction equilibria

It is a familiar finding of island biogeography that a species may be present at any instant on some but not all ecologically suitable islands. These patchy insular distributions are readily interpreted as immigration-extinction equilibria: island populations occasionally go extinct but can be reestablished by immigrations, and the fraction of islands occupied at any instant increases with island area because of decreasing extinction rates (Diamond & Marshall, 1977). Similarly, even in a continuous mainland habitat a local population may occasionally disappear, and the number and extent of vacant patches at any instant should increase with extinction rates and decrease with immigration rates. Most temperate-zone bird species disperse so readily that vacated areas are likely to be recolonized by the next breeding season. Tropical bird species, however, are notorious for their low dispersal ability, so that recolonization of a vacated area may be slow. In addition, extinction rates increase with local species number because of competition. Hence we expect patchiness resulting from immigration-extinction equilibria to be most marked in the species-rich tropics. By this interpretation, patches and gaps should not be fixed but should shift with time.

4. Lockouts

A species may be permanently excluded from an area with suitable habitat by established populations of competitors. Checkerboard distribution patterns on islands, where species replace each other one-for-one, are familiar manifestations of competitive exclusion. Fig. 3 depicts a complex example involving three closely related montane honeyeater species of genus *Melidectes.* When considered individually, each species has a peculiarly disjunct range and is absent from several portions of the New Guinea cordillera. When the ranges of the three species are considered together, however, it is clear that (a) each mountainous area supports two species that exclude the third; (b) the identity of the locally successful combination varies in irregular checkerboard fashion; and (c) each of the three possible combinations occurs in several areas.

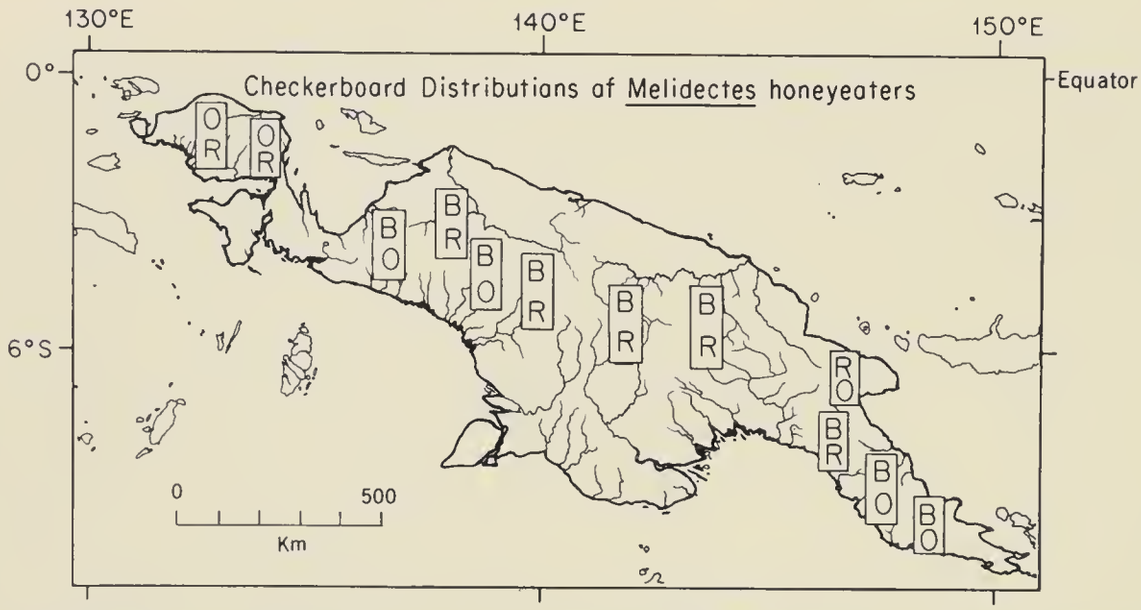

FIGURE 3. Distributions of three Melidectes honeyeaters in the mountains of New Guinea (O = *M. ochromelas,* B = *M. belfordi,* R = *M. rufocrissalis).* Most mountainous areas of New Guinea support two species with mutually exclusive altitudinal ranges. At each locality depicted on the map, the letters above and below indicate the species present at higher and lower altitudes, respectively. (From DIAMOND, 1975.)

I suspect that similar lockouts involving combinations of several species underlie many cases of patchiness in New Guinea (e.g., in the genera *Charmosyna, Tanysiptera, Coracina, Poecilodryas, Pachycephala, Meliphaga, Ptiloprora, Pycnopygius,* and *Melanocharis).* Patches arising from lockouts may occupy the same location for long times. GILPIN & CASE (1976) have shown that competitive lockouts in multispecies guilds are increasingly likely with increasing species richness of the community.

Conclusions

In species-rich tropical areas, many bird species are patchily distributed with respect to available habitat. Likely explanations are based on former (e.g., late-Pleistocene) patchiness of the habitat itself, immigration-extinction equilibria, and competitive lockouts. Each of these factors is more likely to produce patchiness in the tropics than in the temperate zones, and the latter two are more significant in species-rich communities.

Acknowledgments

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Patterns of Foraging Ecology for Common and Rarer Bird Species in Tropical Lowland Forest Communities

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Introduction

The focus of this study will be on patterns of common and rare bird species in tropical lowland forest and will deal principally with interpretations and speculations of ecological causes for the observed patterns (see Karr, 1977). These interpretations will be based on comparisons of data from six sites around the world.

Although being common has some negative attributes such as the potential for high intraspecific competition, spread of disease and parasites, etc., the positive aspects are important. In interspecific competition and colonization, for instance, individuals of large populations often have a dinstinct competitive advantage over individuals of newly arrived, rare species (Simberloff & Wilson, 1969). Common species also often have relatively wide geographical ranges due at least in part to high recruitment rates in marginal habitats and to rapid recolonization of parts of the optimal range decimated by unpredictable density independent factors. Finally, if the chance of extinction is in general inversely correlated with population size, being common can be interpreted as an important character of many populations or species.

Being rare also has advantages. Predators do not readily develop search images and in evolutionary time are less likely to become specialized on rare prey. These rare species can also have a competitive advantage. Minimal direct or indirect interactions with potentially dominant competitors reduce the selective force for characteristics in the dominant competitor that might lead to competitive exclusion.

This report will focus on (1) the number and relative abundance of species on each plot, with descriptions of pertinent characteristics of the common species; and (2) an analysis of ecological characteristics of all individuals of common species combined compared to those of individuals of the rest of the species on each plot.

Methods

The six sites included in this study (three in western Amazonia and one each in Gabon, Papua New Guinea and Indonesian Borneo) are listed elsewhere (Pearson, 1977b) with the physical parameters and the dates and number of hours of observation spent on each. Details of species lists for each site (Pearson, 1972, 1975b, 1975c, 1975d; O'Neill & Pearson, 1974; Tallman & Tallman, 1977; Brosset, 1980) and general ecological patterns have also been published elsewhere (Pearson, 1971, 1975a, 1977a, 1977b).

Each site was located in representative primary forest and consisted of a roughly circular path 2.5—3 km in length. Foliage profiles were similar on the Amazonian sites but somewhat different on the Old World sites (Pearson, 1977b). Foraging birds within 25 m of either side of the path were included for a total area of about 15 ha. All

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observations between 07:00 and 17:00 were included except for raptors and nocturnal species. On sites exhibiting extreme dry season, the end of the dry period and time into the following rainy season were included in the observations. Mist net captures supplemented observation of birds in the low (0—2 m) strata.

Results

Earlier (PEARSON, 1977b) I showed that the number of common species on six tropical lowland forest sites around the world was inversely correlated with the total number of species present. The number of rare species was directly correlated with the total number of species. I defined common (>.12 sightings/hr of observation), uncommon (.12—.08 sightings/hr of observation), occasional (.08—.04 sightings/hr of observation), and rare (<.04 sightings/hr of observation) species as in PEARSON (1977 b). Names of these species on the Old World site are available on request. These data for the New World plots are available elsewhere (PEARSON, 1975, 1977b). Additional species known to occur in the forest but not seen on the study were considered as rare (see PEARSON, 1977b). On the South American sites, all the common species ranged throughout Western Amazonia from Colombia to Bolivia. However, only two species were common on all three sites. On the Gabon site, all the common species had relatively extensive ranges from Western Africa to Eastern Zaire and Uganda. The common species on the Borneo site all ranged from Southern Thailand or the Central Malay Peninsula throughout most of the Greater and Lesser Sunda Islands, except for *Pityriasis gymnocephala,* which is endemic to Borneo lowland forests. On the New Guinea site, all the common species except two had geographic ranges that included most of lowland New Guinea and associated islands. *Psittaculirostris edwardsii* and *Chenorhamphus grayi* had restricted ranges on New Guinea.

To simplify the analysis of patterns among common species, I concentrated on one morphological and three behavioural parameters: (a) mean species weight, (b) foraging technique, (c) vertical use of foliage, and (d) foraging substrate. Obviously these parameters are not totally independent, but they permitted quantification of readily measured characters. Body size is considered important in competition (VAN VALEN, 1973), predation (PAINE, 1976), and efficient use of energy (KENDEIGH, 1972). Foraging technique, vertical stratification, and foraging substrate have been interpreted as important in subdivision of habitat and presumably limiting resources in lowland forests (PEARSON, 1971; KARR, 1976; TERBORGH, 1977; and others), and they may well be involved in predation and physiological aspects as well.

The mean size of common species ranged from 92.0 g on the New Guinea site to 42.5 g on the Gabon site, a 53.8 % variation. The mean size of all species on these sites ranged from 107.8 g on the New Guinea site to 81.9 g on the Borneo site, a 24.0 % variation. The difference between mean weight of common species and all species for each site was obviously made up by the uncommon, occasional, and rare species, which had larger mean weights than the common species on all six plots. There was no significant correlation between the mean weight of common species and that for the rest of the species on each plot ($r_s = 0.31$; $p > 0.05$). The mean weight of the common species, however, was directly correlated with the number of common species ($r_s = 0{,}83$; $p < 0.05$).

More than half of the common species on all but one site (New Guinea) were principally (> 80 % of the observation) gleaners. On the New Guinea site, 24 % of the common species were principally gleaners and 36 % were principally frugivores. On four sites (Ecuador, Borneo, New Guinea, and Gabon) sallying after flying insects was the second most frequently observed principal foraging technique (20 % or more of the common species on each site). The rest of the common species were observed using more specialized principal foraging techniques such as snatching, ant-following, flower (nectar and/or pollen), and pecking and probing trunks and branches. However, only 4—11 % of the common species on a single site were observed using these latter specialized categories as a principal foraging technique. Frugivory was the principal foraging technique for 12 % (Borneo) to 22 % (Peru) of the common species on a plot, except for the previously mentioned 36 % of the New Guinea site.

Differential vertical use of foliage (low, 0—5 m; medium, 5—20 m; high, 20—35 m) was obvious on all the sites for most species in or out of the common category. For the common species, however, the only consistent pattern was that of the relatively few species present on the forest floor. The percent of common species per plot present predominantly (≥ 75 % of observations) at this level ranged from 0 % (Peru) to 26 % (Bolivia). For three plots (Peru, Bolivia, and New Guinea) the greatest percent of common species were present in the highest strata of the forest (20—35 m) and ranged from 42 % (Bolivia) to 89 % (Peru). For the other three plots, the majority of the common species were seen predominantly in the mid-strata (5—20 m) (Ecuador = 43 %; Borneo = 41 %; Gabon = 56 %). No distinct pattern in substrate use by common species was seen on the sites.

Ideally the distribution of common species within these parameters should be compared with that of the rest of the species on each plot. This comparison could then be used to show that the common species were or were not a random sample of the community. The rareness of such a large proportion of the species on each plot, however, resulted in only one to two observations for many species. Any statistical analysis of this comparison would be prohibitively weak. As an alternative, I combined and compared the data from individuals of all common species to those for individuals of the rest of the species on each plot. On the Ecuadur and Peru sites, individuals of the common species made up 36 % of all individuals observed, on the Bolivia site 66 %, on the Borneo site 43 %, on the New Guinea site 70 %, and on the Gabon site 46 %.

I calculated the rank correlation of number of individuals of common species and number of individuals of the rest of the species on each plot using each of nine foraging techniques (glean, sally, snatch, etc., see Pearson, 1977b), seven vertical strata, and 18 substrate categories. On all six sites, individuals of common species used the substrate no differently from individuals of the rest of the species. Significant differences in foraging technique and/or vertical stratification were present on all the sites except the Borneo site. Vertical strata were used differently on the Ecuador, Bolivia, and New Guinea sites. Foraging techniques were used differently on the Peru, Bolivia, and Gabon sites. Where differences in use of vertical strata were significant, they were in low strata and forest floor. Here individuals of rarer species were significantly more prevalent. Where differences in foraging technique were significant, they occurred in the sallying and snatching categories. Individuals of the less common species used mixed sallying and gleaning or snatching and gleaning to a significantly greater degree

than did individuals of the common species. The latter, however, used pure sallying or pure snatching to a significantly greater degree on plots with differences.

Finally I compared the potential correlation between species richness, number of common species, and physical factors of rainfall ($\bar{x}$ annual and number of dry months) and overall foliage density (PEARSON, 1977b). Foliage complexity has been indicated as an important factor in the number of species present in some habitats (MACARTHUR & MACARTHUR, 1961, and many others). More complex habitat supposedly allows finer subdivision of the habitat and thus more species. Rainfall, whether measured in mean annual amount or severity of dry season, had a significant correlation ($r_s = 0.93$; $p < 0.05$) with foliage density (see PEARSON, 1977b). Vertical foliage density, however, had no significant correlation with either the total number of bird species or the number of common species.

Discussion

A search for obvious patterns among common bird species present on these six sites showed little consistency. As was mentioned, the severity of the dry season, the associated synchrony of fruiting and insect emergence (JANZEN, 1967), and the physical complexity of the forest had no correlation with either the total number of species or the number of common species on a site. The lack of patterns is more evident when additional details are emphasized. In forests with similar foliage complexity and different degrees of rainfall seasonality (Peru and Ecuador), there were marked differences in total number of bird species and number of common species. In forests with extreme differences in both seasonality of rainfall and foliage complexity (Bolivia and Borneo or Gabon and Ecuador), the number of common species was similar but the total number of species was different. In forests with similar foliage complexity and rainfall seasonality (Peru and Bolivia), the total number of species was similar, but the number of common species on the Bolivia site was twice that of the Peru site.

Patterns at other levels were also difficult to find. Little convergence was evident in use of vertical strata or foraging technique for common species or rare species from plot to plot. No such evidence was found for substrate use.

Of the few consistent patterns found, wide geographical range was one of the most obvious. Many of the less common species, however, also exhibited extensive geographical ranges. The inverse correlation between mean weight of common species and the total number of a species on a site was another general pattern. This latter pattern may suggest that biomass may be a more realistic measurement by which to measure and compare these sites for patterns. Very likely the greater the number of species, for whatever reasons of geological history and local conditions, the greater the likelihood for competitive interactions. If food, for instance, is limiting, then a reduction in body size among common species might be expected to make subdivisions of habitat and/or resources more feasible (VAN VALEN, 1973). Because individuals of common species would also be the most likely to encounter one another, this selection for smaller size might be more stringent in the common species.

Units of measurement, historical differences in species, input, and other such factors may all be involved in the lack of strong patterns of convergence in characters of common species on these sites. I strongly suspect, however, that the greatest fault of these

comparisons has been in limiting them to birds. In temperate areas and at higher altitudes in the tropics (Diamond, 1973; Terborgh, 1977), the birds are likely so predominant in their communities that this taxocene corresponds well to the limits of significant interactions. The focus on birds as a community in these high latitudes and altitudes approaches reality and patterns become evident. In lowland forests of the tropics, however, the influences and interactions of especially non-avian competitors likely takes on a major role. As I and many other investigators (Harrison, 1962; Charles-Dominique, 1975; Karr, 1976) have indicated, without including non-avian competitors in the analysis of lowland forest communities, the birds may be too small a proportion of the real and interacting community for patterns to be readily determined.

These six plots, for instance, had different numbers of species of frugivorous mammals. An inverse correlation between number of frugivorous mammals and frugivorous birds was evident on all six sites (Pearson, 1975, 1977b). Spiders, damselflies, and birds all shared part of the same base resource continuum of small insects. During some seasons entomophagous fungi left the forest with large numbers of hollow insect exoskeletons. Example after example points to the conclusion that studies of community structure in lowland forests must include many more organisms than birds and their prey.

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Patterns in the Nonpasserine Component of Tropical Avifaunas

John Faaborg

Introduction

Intrigued by the strikingly different metabolic rates exhibited by passerine and nonpasserine birds (Kendeigh, 1972), I did a previous analysis (Faaborg, 1977) that presented three patterns: (1) Nonpasserine species are usually larger than passerines of similar trophic status. (2) There are relatively more nonpasserine species in tropical than temperate regions. (3) Tropical islands have relatively more nonpasserines than tropical mainlands. To try and explain these patterns, a model was formulated which looked at the factors of metabolic demand (energy needed per day), foraging rate (with the assumption that birds with high metabolic rates are more active), resource distribution (assuming large foods are generally rarer than small), and the general population density required for survival. It was suggested that on smaller, abundant resources passerines should have the advantage over nonpasserines because the former's high level of activity allows it to harvest resources more rapidly. Although the passerine may need three times as much energy, if the food is available it should find it and effectively exclude the nonpasserine. As resources get rarer (which may generally include large or specialized types of resources), a threshold may occur where the nonpasserine has the long term advantage over a passerine by being able to expend less energy while searching for the resource and by being able to support larger total populations on a given amount of the resource.

This explanation is compatible with the observations that tropical nonpasserines are larger than passerines, or have larger, more specialized bills, or both. A large portion of the increased avian diversity of the tropics is due to new resources such as large fruits and large insects (Orians, 1969; Schoener, 1971; Karr, 1974). These resources are utilized largely by nonpasserines, so we can also see why nonpasserines should become relatively more scarce in the temperate zone. The relative increase in nonpasserines on islands might be explained by shifting the threshold at which the passerine-nonpasserine change occurs. In the restricted conditions of an island, the larger population sizes maintained by a nonpasserine species may allow it to outlast passerine competitors despite relative inefficiency at foraging.

We can see that there is a distinct nonpasserine component to terrestrial avifaunas. In this paper, I examine some further patterns in the distribution of tropical nonpasserines.

Latitudinal gradients in Nonpasserines

As mentioned earlier, nonpasserine birds tend to monopolize the increase in large resources in the tropics. This explains the general tropical-temperate comparison, but disagreement exists on the characteristics of the change in diversity with latitude. Is there a gradual change in species, or is the decrease in species with latitude precipitous at some point where true tropical conditions end (Schoener, 1971; Klopfer &

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MacArthur, 1961; Tramer, 1974)? Figures 1 and 2 examine the change in the distribution of nonpasserines by size along a latitudinal gradient from Colombia through Mexico. Figure 1 examines frugivores (fruit and seed eaters) while Figure 2 looks at flycatching insectivores.

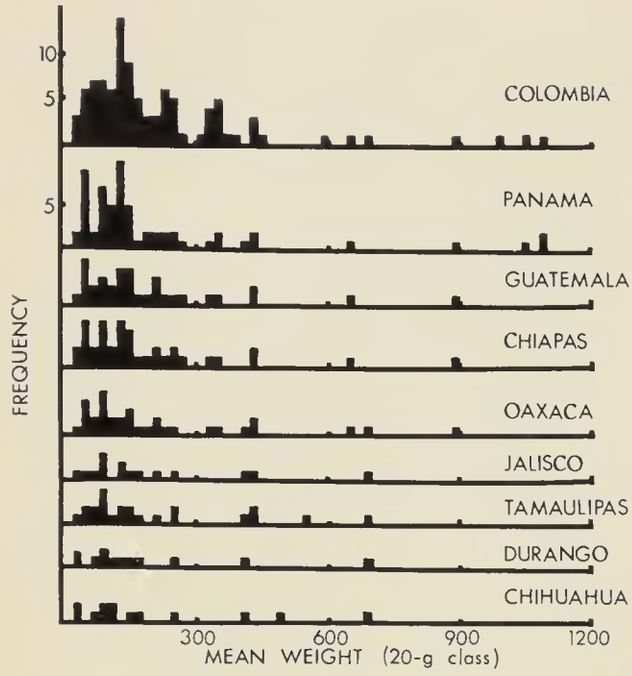

Figure 1. Size distribution of frugivorous nonpasserines along a latitudinal gradient. Families included are Columbidae, Psittacidae, Trogonidae, and Ramphastidae. All the species known for each area are depicted. Mean weights are from the locations cited in Faaborg (1977) or estimated from known weights of similar species. Latitude increases going down the figure. Distributional data are from Meyer de Schauensee (1964), Ridgely (1976), and Peterson & Chalif (1973).

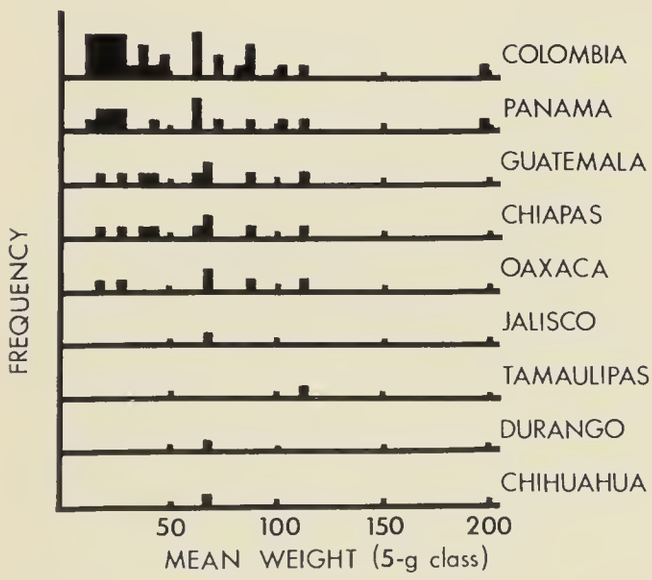

Figure 2. Size distribution of flycatching nonpasserines along a latitudinal gradient. Families included are Momotidae, Galbulidae, and Bucconidae. Data are gathered as in Figure 1.

The number and size of nonpasserine frugivores tends to change gradually throughout the gradient. The largest species disappear north of central Mexico while the frequency of the smaller sizes gradually diminishes. In contrast, the nonpasserine flycatching insectivores show a precipitous decrease in central Mexico. Although not shown, the distribution of nonpasserine gleaning insectivores (the Cuculidae) is intermediate to the guilds shown. A gradual decline occurs from 15 species in Colombia to 7 in Oaxaca, 5 in Jalisco, and only 3 species in the northern states. In both insectivorous guilds the tendency is for the northernmost members of the guilds to be of intermediate sizes.

The difference in pattern between the guilds is most likely explained by differences in the characteristics of the resources used. Fruits and especially seeds are regularly

available throughout the year, while insect densities may vary drastically when far enough north (JANZEN, 1973). The difference between flycatchers and gleaners may be related to the latter's ability to find pupae or perhaps even hibernating insects during cool periods.

Nonpasserine characteristics on land-bridge islands

In the earlier work, I showed how nonpasserines increase in relative importance as the number of species on an island decreases. Several land-bridge islands (islands connected to the mainland by low ocean levels during glacial periods) were included in the data analyzed and these islands generally conformed to the patterns observed for all islands. DIAMOND (1975), TERBORGH (1974) and others have suggested that these islands are undergoing "relaxation", the loss of species with time starting from the supersaturated species number these areas had when they first became islands. It is interesting to see the consistency of the passerine-nonpasserine relationship on the various island types. The above authors and others have suggested that this relaxation phenomenon on land-bridge islands may have important implications for nature preserve design.

If nature preserves surrounded by alien habitat do act like land-bridge islands, we might predict that nonpasserines would be relatively less susceptible to these island effects. This would be misleading, for certain nonpasserine families react very strongly to the effects of insularity. A comparison of species' distributions on land-bridge islands and mainland areas shows the relative susceptibility of a family during relaxation. Table 1 shows the characteristics of linear regressions computed for most of the nonpasserine families found on land-bridge islands of the New World and New Guinea. For each family, the number of species found in the family for each island or mainland area is regressed against the total number of land-bird species in the area. As can be seen, the regressions generally have high correlation coefficients and vary in slope and x-intercept. The x-intercept value is critical, for it predicts the total community size in which the family ceases to exist. In very small communities (less than 40 species) these lines probably become meaningless as these faunas would be characterized by species that are good dispersers. In the larger land-bridge islands, though, these lines are excellent predictors of the types of qualitative changes one might expect as the total species number decreases.

Among New World families, we see that the Ramphastidae and combined Momotidae-Galbulidae-Bucconidae regressions cross the x-axis at 155 species, while the Trogonidae line intercepts at 105 species. Among New Guinea families, the Alcedinidae and Podargidae-Aegothelidae-Caprimulgidae regressions intercept the x-axis at 85 species. All these families could be considered extinction prone. On the other hand, the Columbidae, Psittacidae, and Cuculidae regressions of both areas have lower intercepts, as do several other New World families. It is these families that give nonpasserines a relative advantage in insular conditions. While these data cannot tell us the differences that might exist between nature preserves and land-bridge islands, they do suggest that during relaxation distinct changes occur in the composition of an avifauna.

The above patterns also show how the actual composition of the nonpasserine component varies between New Guinea and the New World. For the three dominant fami-

Table 1: Characteristics of the regression of the number of species in a family with the logarithm of the total number of species in an area or island for nonpasserine families on land-bridge islands or the mainland in the New World and New Guinea area. New World areas included are Honduras (Monroe, 1968), Costa Rica (Slud, 1964), Surinam (Haverschmidt, 1968), Guatemala (Land, 1970), Trinidad (ffrench, 1973), Coiba (Wetmore, 1957), San Jose (Wetmore, 1946), and Rey (MacArthur, Diamond & Karr, 1972). New Guinea data are from Rand & Gilliard (1967) and include New Guinea, the Aru Islands, Misol, Salawati, Waigeu, and Japen. In some cases families of similar trophic status are combined. The x-intercept of the regression may predict the community size at which a family should cease to be present.

Family	Slope of regression	Correlation coefficient (r)	x-intercept (no. of Species)
New World			
Columbidae	15.2	0.94	28
Psittacidae	14.5	0.87	37
Cuculidae	6.7	0.93	30
Nyctibiidae-Caprimulgidae	6.7	0.92	33
Trochilidae	36.9	0.92	30
Trogonidae	12.7	0.92	105
Alcedinidae	3.1	0.91	17
Momotidae-Galbulidae-Bucconidae	28.5	0.92	155
Ramphastidae	12.5	0.87	155
Picidae	13.9	0.95	42
New Guinea			
Columbidae	25.9	0.94	19
Psittacidae	51.8	0.98	68
Cuculidae	14.6	0.96	54
Podargidae-Aegothelidae-Caprimulgidae	14.4	0.95	85
Alcedinidae	14.4	0.95	85

lies found in both areas (Columbidae, Psittacidae, and Cuculidae), the land-bridge island regression is much steeper in New Guinea than it is in the New World. Relatively few nonpasserine families make up a larger portion of the avifaunas of the New Guinea region. Yet, in mainland situations in both areas the proportion of land-bird species that are nonpasserine is remarkably constant. Five South or Central American countries with from 365 to 486 listed species have between 32.3 % and 34.8 % nonpasserine species. The avifauna of New Guinea (including land-bird species only) is 30.3 % nonpasserine, that of Borneo is 34 % nonpasserine, and Viet Nam has 30 % nonpasserine species. Thus, while we can make some generalizations about passerine-nonpasserine interactions that seem to always hold in complex faunas and regularly hold on islands, the detailed characteristics of this nonpasserine component of tropical avifaunas vary regionally.

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Feeding and Breeding Strategies of Sympatric Terns on Tropical Islands

Kees Hulsman

Introduction

The tropics have slightly fewer species of marine tern (18 species) than the temperate regions (21 species). Of these 8 species breed in both tropical and temperate regions (Clements, 1974). Despite the fewer species of tern in tropical regions, more species breed sympatrically in the tropics than in the temperate regions (Table 1). My question is: why do more species of tern breed sympatrically in the tropics than in the temperate regions?

Offshore and inshore feeders

One reason is that temperate regions lack offshore feeders (Table 1). What are the characteristics of inshore and offshore feeders? Inshore feeders often have a clutch of more than one egg and a short incubation period. Their chicks receive small amounts of food frequently and have a fast growth rate. Adults hunt close to their colonies and carry food in their bills to their young, and they first breed when they are 2 to 4 years old; e.g. Common Tern *Sterna hirundo* and Sandwich Tern *S. sandvicensis* (Table 2; Lack, 1968). Offshore feeders have a clutch of one egg and a long incubation period. Their chicks are capable of handling large infrequent feeds and have a slow growth rate. Adults may hunt far from their colonies and regurgitate food for their young, and they have deferred maturity; e.g. Bridled Tern *S. anaethetus* and White-capped Noddy *Anous minutus* (Table 2; Lack, 1968).

Table 1: Number of tern species nesting on some tropical and temperate islands

TROPICAL			TEMPERATE		
Island	Offshore	Inshore	Island	Offshore	Inshore
Ascension	3	0	Petit Manan	0	3
Christmas	4	2	Great Gull	0	3
Bikar	5	3	Wangeroog	0	2
One Tree	2	4	Griend	0	4
Aldabra Atoll	2	2	Coquet	0	5

Inshore feeders probably evolved in temperate regions where food was abundant near colonies for a short part of the year. Long hours of daylight provide adults with more time in which to hunt than is possible in the tropics; they can raise several young simultaneously in a short time. Offshore feeders probably evolved in tropical environments where food was extremely patchily distributed and birds flew long distances in search of prey. The short day-length greatly reduced the time available for hunting. Associated with these two conditions are the slow growth rates of chicks and their tolerance to go without food for several days. Predation on young may be a reason why

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young of temperate terns have fast growth rates, but terns could not adopt this strategy unless food was common. Offshore feeders by nesting under or in vegetation reduce pressure from avian predators on eggs and young (HULSMAN, 1977).

Tropical inshore feeders, e.g. the Roseate Tern *S. dougallii*, lay smaller clutches than their temperate counterparts (Table 2). The reduction in clutch size of inshore feeders in the tropics probably resulted from their inability to catch enough food during 12 hours of daylight to raise two or more young simultaneously. If reduction of clutch size indicates how long a species has been in the tropics (Table 2), then there have been successive invasions of the tropics by temperate species of tern.

TABLE 2: Some characteristics of breeding tropical and temperate species of tern. (T) = temperate species, other data from tropics

Species	Clutch size	Incubation period (days)	Fledging period (days)	Nest-area	Feedings/ dependent/hour
Roseate	1.1 ± 0.3[1]	21—24	27—30[2]	open-veg.	
(T) Roseate	1.7 ± 0.2[2]				
Black-naped	1.5 ± 0.1	21—23	28	open	0.83 ± 0.53 (16)
(T) Common	2.6 ± 0.3[3]	21—26	23[4]	veg.	0.85 ± 0.60[3] (18)
(T) Sandwich	1.5 ± 0.5[5]	23	27[4,5]	open	0.81 ± 0.62[3] (18)
Lesser Crested	1.0	21—25	32—35	open	0.89 ± 0.60 (12)
Bridled	1.0	28—30	61—63	veg.	0.31 ± 0.12 (7)
White-capped Noddy	1.0	35[6]	45[6]	tree	0.30 ± 0.11 (16)

[1] E. CAMERON, pers. comm.; [2] NISBET & DRURY, 1972; [3] LANGHAM, 1974; [4] PEARSON, 1968; [5] VEEN, 1977; [6] ASHMOLE, 1962; other data from HULSMAN (1977). Sample size refers to derived data.

Here the order of colonization is unimportant; I am concerned with colonization. Some of the colonizing species are now extinct in temperate regions. Possibly the rate of extinction is greater in temperate regions than in tropical ones (see TERBORGH in this symposium). If so, one expects more species to have restricted distributions in temperate regions than in tropical regions (Table 3). This poses the question: why is the rate of extinction retarded in the tropics? The answer lies in the patterns of resource availability; perhaps availability is reflected by abundance.

TABLE 3: Distribution of terns breeding in tropics, temperate regions or in both regions

Distribution	Temperate	Tropical	Temperate & Tropical
restricted	9	2	4
patchy	2	5	3
wide	2	3	1

Pattern of resource availability

Tropical oceans have a low productivity per unit area and near the equator food is available at a relatively constant level (ASHMOLE, 1971). Some terns may breed sub-

annually: e.g. Bridled Tern every 7.5 months (Diamond, 1976) and Sooty Tern *S. fuscata* every 9.6 months (Ashmole, 1963). Further away from the equator, terns breed annually. In sub-tropical regions there is a distinct annual cycle of productivity in the sea. At One Tree Reef, there is a distinct peak in photosynthetic activity between January and May (Kinsey & Domm, 1974), and juvenile recruitment of reef fishes between January and February (Russell et al., 1977). But the period of increasing productivity and recruitment (hence breeding) is spread over 8 to 9 months of the year. This pattern of productivity (Fig. 1) enables the use of the food supply by both inshore and offshore feeders. Inshore feeders use the bloom and offshore feeders use the long period during which food is available. I expect that near the equator the peak in productivity (Fig. 1) flattens out, and that in the temperate regions the peak becomes more pronounced but productivity restricted to, for example, four months of the year.

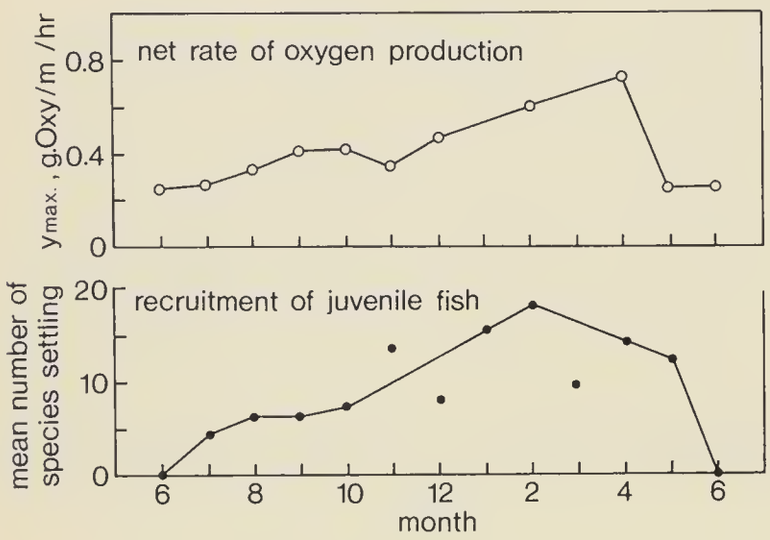

Figure 1. Net rate of oxygen production at One Tree Reef 1972. Y max is the net rate of oxygen production at midday. February reading from experimental pool 1971, control pool 1972 gave similar readings as experimental pool in other months (from Kinsey & Domm, 1974). Juvenile recruitment of reef fishes 1972—1975 (from Russell et al., 1977).

The means of segregation among terns differ from one locality to another. Some of the differences are caused by the different patterns of resource abundance during the year. To illustrate this I shall compare the community of terns at One Tree Island (23° 31′ S, 152° 06′ E) with that at Christmas Island (2° N, 157° W).

One Tree Island vs Christmas Island

One Tree Island supports 4 inshore and 2 offshore species whereas Christmas Island supports 2 inshore and 4 offshore species.

(1) Segregation by the size of prey eaten is more pronounced among terns at One Tree Island than among those at Christmas Island (Fig. 2). The slopes of the regression lines describing the relationship between width of the gape of terns and the length of their prey at One Tree and Christmas Islands are significantly different ($t = 4.66$, df 9, $p < 0.005$). Lesser Crested Terns *S. bengalensis* and Crested Terns *S. bergii* are segregated from one another, as well as from the smaller terns, by the size and type of prey that they eat (Hulsman, 1977). At Christmas Island, the Blue-grey Noddy *Procelsterna cerulea* is segregated from other terns by the size and type of prey it eats (Ashmole & Ashmole, 1967).

(2) Segregation by distance that species hunt from their colonies is important for some species at both localities; i.e. offshore vs inshore feeders. The three small species

of tern at One Tree Island (White-capped Noddy, Roseate Tern and Black-naped Tern *S. sumatrana*) are segregated by the distance which they can hunt from their colonies and by their methods of foraging, as are the Sooty Tern and the Common Noddy *A. stolidus* at Christmas Island. Noddies depend on predatory fishes to keep their prey available whereas the other terns do not rely solely on predatory fishes for the availability of their prey (HULSMAN, 1977).

(3) The White Tern *Gygis alba* is segregated from other offshore species by its mainly hunting at dusk and dawn (ASHMOLE & ASHMOLE, 1967).

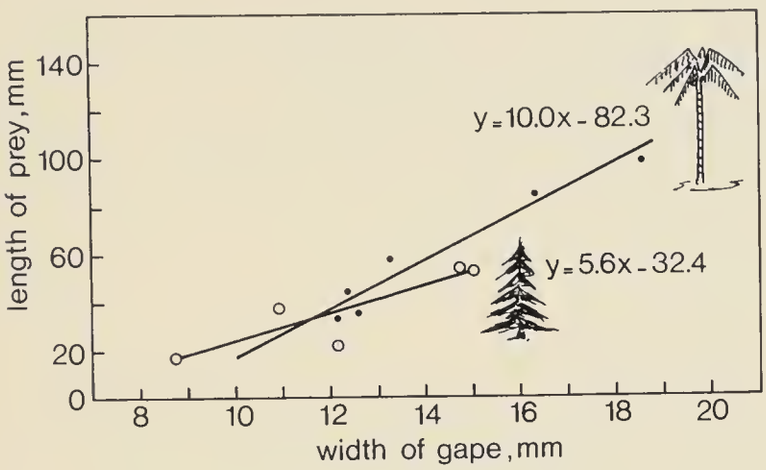

FIGURE 2. Relationships between the mean width of the gape and the mean length of prey eaten by terns at One Tree Island ($Y = 10.0(\pm 1.2)X - 82.3$, $p < 0.005$) and Christmas Island ($Y = 5.6(\pm 1.9)X - 32.4$, $p > 0.05$).

Ratio of offshore to inshore species

Near the equator, the number of offshore species should be greater than the number of inshore species, if the pattern of food abundance is important. Away from the equator, inshore species should become more common than offshore species. At Aldabra Atoll (9° 24′ S, 46° 20′ E) in the Indian Ocean the ratio is 1:1 (DIAMOND, 1971) as it is on the Great Barrier Reef (KIKKAWA, 1976). But at Christmas Island (ASHMOLE & ASHMOLE, 1967) the ratio is 2:1, and in the Northern Marshall Islands (9°—14° N, 161°—171° E) offshore species outnumber inshore species 3:1 (FOSBERG, 1966). What factors determine the number of species breeding on an island?

LACK (1968) argued that offshore feeders can nest in few large colonies (safe from predators) because they travel such large distances in search of food. Conversely, LACK

TABLE 4: Distribution of offshore and inshore feeders nesting on islands in the Capricorn and Bunker Groups; data from KIKKAWA (1976)

CAPRICORN GROUP			BUNKER GROUP		
Island	Offshore	Inshore	Island	Offshore	Inshore
One Tree	2	4	Fairfax	2	5
Wilson	0	3	Lady Musgrave	2	2
Wreck	1	1	Hoskyn	2	0
Heron	1	1			
Tryon	2	2			
Masthead	2	2			
North-west	2	1			

(1968) argued that inshore feeders, which travel short distances in search of food, nest in many small colonies close to their hunting grounds. In the Capricorn and Bunker Groups of the southern end of the Great Barrier Reef, offshore and inshore species nest on all but one island each (Table 4). According to LACK's reasoning, offshore species should be nesting on a few of the islands, not most of them, unless nest-areas are in short supply.

Inshore species nest in the open (e.g. Black-naped and Lesser Crested Terns) whereas offshore species nest in or under vegetation (e.g. White-capped Noddies nest in trees, and Bridled Terns nest under low shrubs). Most of the islands in the Capricorn and Bunker Groups have trees and shrubs suitable for noddies and Bridled Terns to nest in, but the islands do not all have suitable open areas for the inshore feeders to nest in. Both One Tree and Fairfax Islands, which have the greatest number of species nesting on them, have vegetation and open areas. Thus it is the availability of suitable nest-areas for terns that determines the number of species nesting on an island via the grace of an ample supply of food.

Conclusion

More species of tern breed sympatrically in the tropics than in temperate regions because the pattern of food availability effectively enlarges the tropical environment compared to the temperate one. Thus potentially more species can coexist in the tropics. The actual diversity on an island is determined by the availability of suitable nest-areas.

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SYMPOSIUM ON
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CONVENER: ALLAN KEAST

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History of the Habitat Concept in Birds and the Measurement of Avian Habitats

James R. Karr

Introduction

Like most ornithological science the study of habitat use by birds has matured rapidly in recent decades. But what is meant by "habitat"? Unfortunately, the word is used in conflicting ways (Whittaker et al., 1973), leading to some confusion. The most popular use is as a description of the environment of a species or community; as a shorthand this often becomes a vegetation type in terrestrial environments. (Note that analogs exist in aquatic and marine environments where vegetation is a subordinate or absent habitat component.) Some object to this general use of the word, and restrict habitat to the set of physical and chemical conditions which surround an organism (Kendeigh, 1974); others include both the living and non-living surroundings (Smith, 1974), the equivalent of biotope of Kendeigh (1974) and the common usage in Europe.

All of this focusses on the human perception of habitat when, in fact, it is the bird's perception that is of evolutionary interest. Birds may differentiate habitats by selection of specific horizontal (vegetation type) or vertical (twig angle, leaf density) components of habitat gradients, but the concept of habitat as a vegetation type recognizes only the horizontal component. Similarly, habitat (bird-perceived) use by a bird may change as competition dynamics shift (island vs. mainland, MacArthur et al., 1972) while the vegetation type in two areas remains essentially the same. Finally, the precision of segregation along vertical and horizontal (Karr, 1976a) gradients varies geographically, leading to confusion when the two uses of habitat are not clearly segregated. The two meanings should be clearly distinguished in the future to avoid ambiguities. Initially and for historical purposes, I shall define habitat as the vegetation type (plant community) characteristically occupied by a bird.

Historical sketch

Three more or less distinct stages might be recognized in the development of studies of avian habitats. The first "Catalog Stage" began with efforts to identify birds and determine their phylogenetic and biogeographic affinities. Habitat descriptions were generally cursory and non-quantitative. For example, the monumental Manual of Neotropical Birds (Blake, 1977) describes the habitat of the Red-tailed Hawk *Buteo jamaicensis* as "Mainly woodland and semiopen country."

During the second "Natural History Stage" scientists were interested in the general biology or natural history of species. Details such as nest type and location, food habits, clutch size, incubation period and general habitat were of primary interest. There was a clear interest in the habitat associations of birds but few efforts were made to provide quantitative information on avian habitats; the main focus was the bird itself. The classic and monumental works of Nice (1937) on the Song Sparrow *Melospiza*

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melodia and SKUTCH (e.g. 1969) on neotropical birds are examples which focus on the natural history of birds, including non-quantitative studies of their habitats.

In the third "Ecology of Habitat Stage" emphasis shifted with interest in both the birds (often as communities) and their habitat (vegetation type). Early efforts include the pioneering works of MERRIAM (1890), GRINNELL (1917), LACK (1937), PITELKA (1941), KENDEIGH (1945), and SVÄRDSON (1949). These workers recognized the importance of foliage structure in determining avian use of habitat, but not until the pivotal paper of MACARTHUR & MACARTHUR (1961) did a formal quantitative approach develop. MacArthur "merely" provided a quantitative and graphical demonstration that vegetation of increasing height and complexity typically supports increasingly diverse avifaunas. Many refinements of this approach have been developed in the past 17 years. Some are appropriate for consideration of single species while others are more appropriate to community level studies.

Increased emphasis on quantitative approaches to the study of avian habitats has precipitated some innovative uses of quantitative methods. The use of information theory was pioneered by MACARTHUR and has continued with the work of others (Fig. 1; RECHER, 1969, KARR & ROTH, 1971, BLONDEL et al., 1973). Other efforts to demonstrate a relationship between foliage height diversity and bird species diversity have

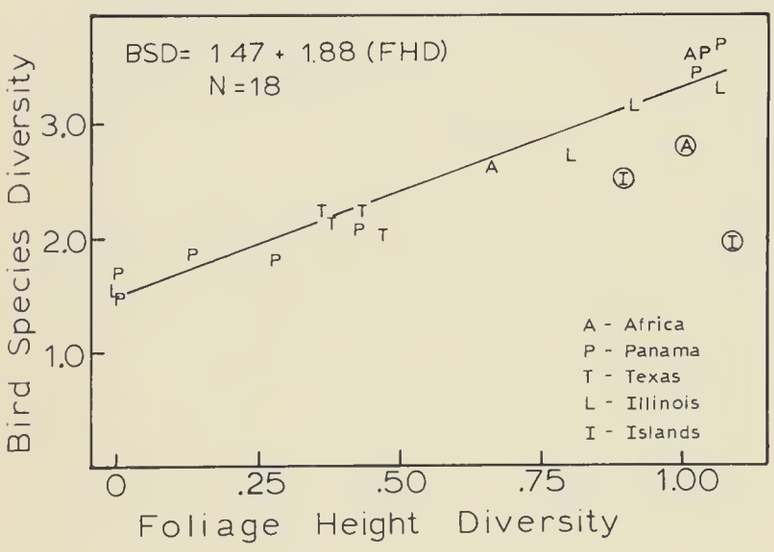

FIGURE 1. Regression of bird species diversity on foliage height diversity from several geographic areas (modified from KARR & ROTH (1971) with additional data). Circled observations are oceanic or ecological islands.

been less successful. Some failed because of inappropriate measures of habitat structure. Others failed in habitats where the rules of plant geometry and distribution are different. For example, foliage volume is important in some situations (STURMAN, 1968; LAUDENSLAYER & BALDA, 1976), while life form diversity of plants is more important in others (TOMOFF, 1974). Further, the relationship between habitat structure and avian diversity is often less precise when narrow ranges of habitat structure are examined (LOVEJOY, 1974; WILLSON, 1974). I make an appeal here for researchers to ask not whether their results support "MacArthur's relationship", but why they do or do not. Why, for example, do the relationships hold for some regions and habitat types but not for others? How do the availability of food resources, nesting sites, and other correlates of vegetation structure change within and between habitats and affect habitat use by birds?

In some cases there is evidence that the quantitative nature of the information theoretic measure of diversity produces peculiar results. BSD in species-rich tropical forest is not high relative to less species-rich temperate forest faunas (Karr & Roth, 1971) due to the behavior of the index in systems with many relatively rare species. Problems may also develop with the presence or absence of certain classes of food resources. In the lowland tropics, for example, availability of soft-fleshy fruits and nectar resources has a major impact on avian community structure without much effect on foliage height diversity (Karr, 1971, 1976a; Terborgh, 1977).

Another important factor determining avian habitat use is "ecosystem patchiness". This may be patchiness in time such as that exhibited in seasonal pattern or year to year variation (Karr, 1976b, 1980; Wiens, 1977). A second component of patchiness might be referred to as spatial heterogeneity (patchiness in space—Roth, 1976; Wiens, 1976).

In summary, the use of the information theoretic measure of diversity in avian community studies has yielded considerable insight (and more refined questions) about the bird-habitat relationship. This is especially true when first order patterns between habitats with major differences in vegetation are examined and where a small number of biological variables are important in determining community structure (or where a number of variables are associated with vertical components of vegetation). The procedure allows a quantitative means to scale changes in habitat against changes in avian communities. Disadvantages of the approach are the requirement of revisions in certain problem habitats such as determination of plant volume diversity or life form diversity. Finally, it is difficult to work with second order patterns such as among a number of forests with differing water regimes or in disturbed areas. In general, research in this field has progressed beyond the calculation of a single index or the construction of straw-man arguments using the "MacArthur relationship".

An array of multivariate statistical procedures are also being used in studies of bird-habitat relations. In general these techniques (principal components, discriminant function, reciprocal averaging, canonical correlation) have the attribute of reducing a number of variables to a small set of complex variables. Other attractive features include easy development of graphical presentations and studies of how variation in one variable affects birds when other variables are held constant (Karr & James, 1975).

Multivariate methods are not without problems however. First, like most univariate methods, they are merely descriptive procedures. They are essentially correlation techniques and cannot be used to determine causal (ultimate or even proximate) relationships between birds and their habitats. Although complex data transformations result from use of multivariate procedures it is not always clear how to extract biological (vs. statistical) meaning from the correlations. Further, the caution that ecology is the art of describing the obvious is also relevant. There is a tendency to use multivariate methods to demonstrate phenomena which are already obvious from univariate studies. The true test of a procedure is its ability to generate new predictions about biological phenomena, to go beyond the obvious. Application of multivariate methods cannot substitute for in-depth consideration of the biology of the organisms under investigation. Careless use of these procedures has stimulated one biologist to comment that so much mathematical formality combined with so much ecological casualness is puzzling (Beals, 1972).

I caution users of principal components analysis (PCA) to use care in interpreting the significance of variance accounted for from a multivariate data set. One study (WHITMORE, 1977) examined the relationship between 10 habitat (vegetation) variables and 24 bird species using PCA and found 85 % of the variance in the data set accounted for by the first three principal components. Fifty-five percent of the variance in a similar matrix of random numbers was accounted for by the first three principal components (Table 1). The true test of a procedure is the production of biological insight and not accounted for variability.

TABLE 1. Cumulative percent of variation accounted for by principal components I, II, and III in two data matrices. Both matrices are the same size (24 × 10).

Principal component	Data matrix: Random number table	Data matrix: Vegetation (10) and bird (24 spp.) table
I	22	56
II	41	73
III	55	85

Finally, some researchers have equated the results of a multivariate study of vegetation structure to the n-dimensional niche of HUTCHINSON (1957). Despite their multidimensional similarity they are not the same. What is being measured is a number of components of the vegetation (narrowly defined habitat niche) and not the Hutchinsonian niche.

In summary, multivariate methods have considerable potential to yield insight about the bird-habitat relationship if they are used to generate predictions (hypotheses) and not simply as descriptive measures. Unless new biological insights are generated by their use, I doubt they have value in ornithological science. (Once we understand the causal relationships determining bird use of an area, multivariate descriptors should have use in a number of resource management contexts (SHUGART et al., 1975).)

Morphology and habitat

Another major aspect of birds and their habitats that has received attention in recent years is the study of correlations between bird morphology and habitat type. General relationships between trophic apparatus (the bill) and food resources have long been recognized (LACK, 1947). More recently there has been a resurgence in the study of morphology as an indicator of selective pressure deriving from habitat characteristics. Over 20 years ago DILGER (1956) showed relationship between tarsal length and ecology in thrushes. Recently KARR & JAMES (1975) explored the relationships between morphology and ecology in forest birds. On a finer scale PEARSON (1977) has shown how wing and leg length and other morphological characters are molded by vegetation structure in antwrens. Some of the most detailed studies of these relationships have been conducted by LEISLER (1975, 1977a, 1977b) on several genera of warblers in Europe. LEISLER's work shows that we have barely scratched the surface of the fascinating relationship between habitat and bird morphology.

Problems of measuring habitats

Ideally, I would like to be able to offer a discrete and manageable protocol for the measurement of avian habitats. However, we simply are not at the stage where that is possible. Further, I doubt that it will be possible except in narrowly defined studies with specific objectives. The choice of factors to be measured must be defined by the objectives of the study, the type of bird under consideration, and how the birds perceive and use their habitat. These general statements are true for both what is to be measured and how it is measured. Researchers should always keep in mind the problem of scaling (COLWELL & FUTUYMA, 1971). A study of avian communities along a habitat gradient (grassland to forest) might find vegetation density in three (herb, shrub, and tree) levels adequate but that is clearly not the detailed scaling needed for the study of *Acrocephalus* warblers.

Detailed procedures with many attractive features have been proposed by EMLEN (1956) AND JAMES & SHUGART (1970). I have used a simpler procedure in which vegetation density is measured over a number of height intervals. This method (KARR, 1971) has proved to be successful both in community studies and also in studies of single species. Using this procedure PAIGE (unpub.) showed a significant difference in the vegetation density between used and unused areas in Ruffed Grouse *Bonasa umbellus*. Vegetation was denser between 2 and 7 feet in used (63 % cover) than in unused (38 % cover) areas. Heights below 2 feet and above 7 feet did not have different vegetation densities. Researchers should incorporate portions of the EMLEN, KARR, and JAMES & SHUGART methods with their own innovations to meet their own study objectives.

Birds and their habitats: The future

Numerous studies have demonstrated special circumstances which modify the relationships between birds and their habitats. For single species or entire communities a bewildering variety of variables are relevant to different extents among habitats and geographic areas. It is clear that future efforts to understand the ecology of habitat use in birds must expand the definition of habitat use to include the widest possible range of environmental factors which affect a bird's use of a specific area. The number of factors which might be relevant is awesome. Restricting consideration to terrestrial environments I can propose a tentative set of primary variables and their interactions (Fig. 2).

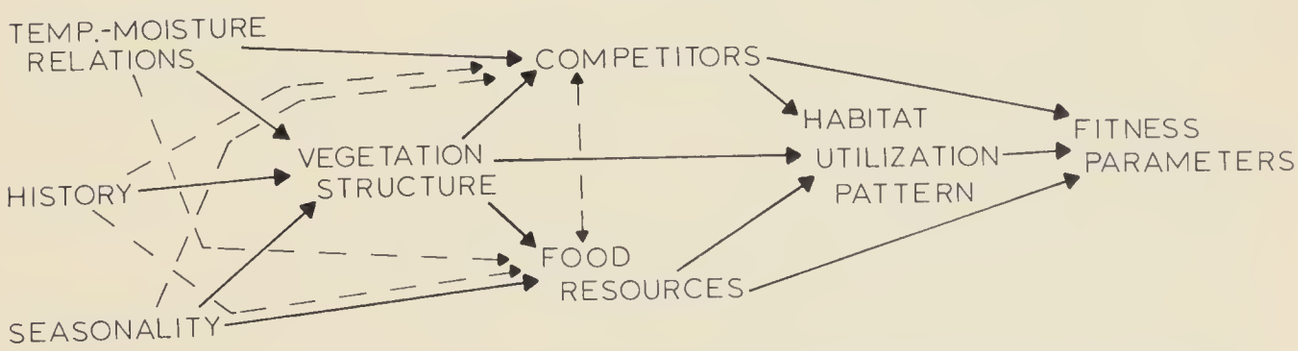

FIGURE 2. Primary factors (and their interrelations) which affect birds and their habitats.

Limitations of space do not allow detailed discussions of these variables. The following outlines some of the factors that seem to be relevant to these primary variables but many others should no doubt be considered.

Temperature-Moisture Relations—Mean annual temperature, rainfall, and evaporation; water availability.
History—Long and short term historical factors.
Seasonality—Periodicity of temperature and rainfall; duration and severity of lean seasons; predictability of transitions between "seasons".
Vegetation Structure—Vertical and horizontal components; special nest and display sites.
Competitors—Number and type; taxonomic group.
Food Resources—Types; abundances; spatial and temporal distribution.
Habitat Utilization Pattern—Generalist vs. specialist; niche breadth and overlap; morphology; behavior.
Fitness Parameters—Reproductive success.

The key messages in this hierarchy, in my opinion, are as follows. While vegetation structure is often an accurate index of habitat quality, advances in the analysis of habitat suitability and use must focus on the potential niche structure of the community, rather than vegetation structure, the first approximation to that. Habitat quality must be measured as an ability to provide a multidimensional set of resources which affect the fitness of individuals using a habitat.

Finally, when the approach is a community study it is important to recognize that habitat suitability will vary independently among a set of guilds within the community (Karr, 1976a, b). Recognition of this along with the phenomenon of patchiness in space and time will result in a more dynamic and, hopefully, more accurate view of birds and their habitats.

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Habitat and Locality Selection in Lesser Snow Geese: The Role of Previous Experience

F. Cooke and K. F. Abraham

The habitat selection process in birds probably has both a genetic basis and a learned component. Klopfer & Hailman (1965) demonstrated that wild-caught adult Chipping Sparrows *Spizella passerina* preferred pine foliage over oak leaves in a choice situation. Kaspar-Hauser reared young also showed this preference, indicating that it was genetically based. In both cases the preference was not absolute and considerable individual variation in choice occurred. Young reared among oak leaves, however, spent a relatively smaller proportion of their time in pine. This points to the role of experience in modifying habitat preferences. Hilden (1965) similarly emphasizes the role of learning in habitat selection.

Given phenotypic variation in habitat selection and provided that some of this variation has, or has had, some genetic basis, then evolutionary theory would predict that natural selection would favor those individuals able to detect and utilize habitats which maximize their reproductive output.

Fretwell & Lucas (1970) developed a number of theoretical models which linked habitat utilization and reproductive fitness, and a great many studies have shown that reproductive fitness within a species differs among different habitats. Robertson (1972), for example, showed that nesting success of Redwinged Blackbirds *Agelaius phoeniceus* was considerably higher in marsh habitat than in upland habitat. He suggested three possible hypotheses to explain habitat selection in redwings: (1) site tenacity of adults and habitat imprinting on nestlings resulting in their faithful return to natal habitat type; (2) preference for the optimal (i.e. marsh) habitat by all individuals; and (3) site tenacity of adults breeding for the second and subsequent occasions and habitat selection for the optimal habitat by first-time breeders. These different hypotheses would result in differing degrees of gene exchange between the populations and would necessitate alternative predictions about the population consequences of habitat selection. On a priori grounds Robertson preferred hypothesis (3), but without an individually marked population of birds it was impossible to resolve the question.

Long-term studies with marked individuals are clearly necessary for a resolution of the role of learning in habitat selection. The work which we have been carrying out with Lesser Snow Geese *Anser caerulescens caerulescens* in the Canadian Arctic is a 10 year study and we are in a favorable position to investigate the role of previous experience in habitat selection. Following Immelmann (1975) we have differentiated between habitat selection and locality selection. The former relates specifically to a visually distinct structural unit of the environment, e. g. marshland vs. upland field. Locality selection refers to a particular segment of habitat, Marsh A as opposed to Marsh B.

To what extent are the selections made influenced by previous experience? We have shown elsewhere (Cooke, 1978) that previous experience has a considerable effect on the way in which mates are selected and it has been possible to extend this type of analysis to habitat and locality selection.

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The Snow Goose colony at La Pérouse Bay, near Churchill in northern Manitoba, consists of 3,000—3,500 pairs of breeding geese. Over 40 % of the adult females are individually color marked thus allowing large samples of birds to be followed through several stages of their life.

Data were collected each year since 1968 by finding as many nests as possible in the colony. Nests were monitored throughout initiation, incubation and hatch. Nest locations were mapped on aerial photographs and given precise Cartesian co-ordinates to allow computer analysis of nest placement between and within years. At hatch, goslings were web tagged so that their natal nest and family were known when later caught at banding, approximately four weeks after peak hatch. Approximately 4,000 adult geese and goslings are banded each year with color bands to allow recognition of birds at the nests.

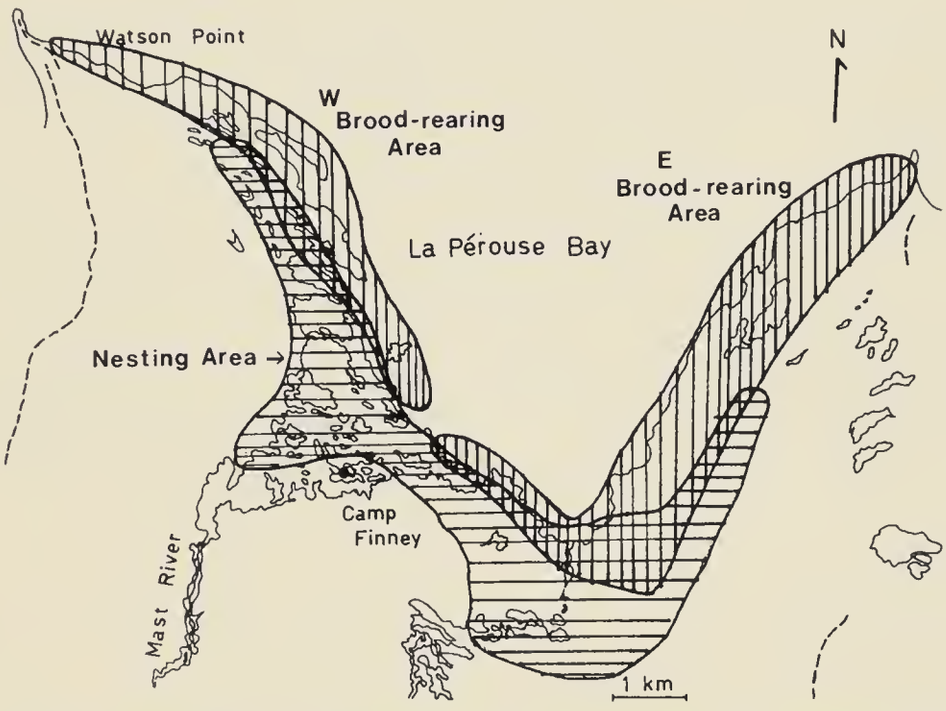

Figure 1. Nesting and feeding areas of Snow Geese at La Pérouse Bay.

Fig. 1 shows the geography of the colony. The nest area extends approximately 8 km along the shore of Hudson Bay. The nesting area is constricted in the middle by the Mast River and there are easterly and westerly nest concentrations. Nests are located on islands in the delta and on the adjacent mainland. Nest sites are found in three basic habitats. These are (1) short willow *(Salix brachycarpa)*; (2) Lyme grass *(Elymus arenarius)*; and (3) assorted short grasses (mainly *Calamagrostis neglecta*). Although generally the willow predominates further from the coastline, all vegetation types can be found in close proximity in most parts of the colony due to dissected topography. Seaward of the nest areas are two feeding areas separated from one another by the waters of the Mast River. These areas are salt marshes occasionally flooded by sea water and consisting predominantly of *Carex salina* and *Puccinellia* spp. which provide the bulk of the food for the birds after hatch.

There are considerable differences in the nest success among the habitat types and habitats used, *Elymus* areas being less suitable than the others. This is demonstrated here with data from 1976 and 1977. Firstly, the proportion of unsuccessful nests and

the levels of predation and abandonment were significantly higher, and final clutch size was lower, in *Elymus* in both years. Secondly, the utilization of habitats differed because of different patterns of snow disappearance. The norm for our ten year study was typified by 1976; birds arrived while snow covered the bulk of the colony and gradual snow disappearance restricted availability and acquisition of nest sites. Habitat and nest site availability were not restricted by snow cover in 1977 as birds arrived two weeks after all snow had disappeared. Thus 1977 was a year of maximum choice for nesting geese. The proportion nesting in *Elymus* was considerably lower in 1977 (13.3 %) than in 1976 (34.7 %). Of 141 individually marked birds seen in the two years, 64.5 % were in the same habitat in both years but a substantial number, 25.5 %, moved from *Elymus* in 1976 into either willow or short grass in 1977. It seems clear that according to these measures *Elymus* is an inferior nesting habitat.

We would next like to consider nest locality in the colony. All three habitat types are available throughout the colony and so a bird seeking willow habitat still has many possible localities in the colony. How is nest locality chosen by the birds? Does previous experience influence the decision? A second and closely related question is the choice of feeding area. How is it chosen and does previous experience influence the decision? The data will be primarily for female geese since we have earlier shown (Cooke, MacInnes & Prevett, 1975; Cooke & Sulzbach, 1978) that whereas adult female geese usually return to breed in the same colony in successive years, males return only if their mate returns. Similarly females hatched at our colony generally return to breed whereas males virtually never do so. This is because pair formation, which is generally for life in snow geese, occurs on the wintering area or during spring migration when birds from many different colonies mix. The female determines which colony to return to, if the two members of the pair are from different colonies. Similarily the female makes the decision about choice of nest locality and post-hatch feeding area.

A word about the life history is necessary for a comprehension of the subsequent analysis. On hatching, the goslings and parents remain at the nest site for around 24 hours. The family group then leaves for the feeding area where the young birds grow rapidly while the adults undergo wing moult. The birds leave the breeding area in August or September and family groups migrate south together and, if they survive, return together the following May. The young birds, now yearlings, leave the adults who then establish a territory and raise another brood. The yearlings spend the incubation period on a feeding area but visit their parents occasionally, being tolerated in the parental territory. At the time of hatch the yearlings, together with other non-breeders and failed breeders, undergo a northward moult migration (Abraham & Cooke, in prep.). First pairing usually occurs in the second winter and a variable proportion of the two year olds return to breed (Finney & Cooke, 1978). By the third year of life most birds are capable of breeding.

The first question to be asked is whether there is any evidence of nest locality tenacity within the colony. This can be answered by tabulating the distance between nests of known birds in successive years. It must be noted that this clearly excludes birds which have left the colony completely, probably a small proportion of the females (Cooke & Sulzbach, 1978), and it refers overwhelmingly to successful nesters, since the color bands which allow individual recognition are usually identified only at hatch. Fig. 2 shows the data in comparison with what one would expect if birds moved randomly

within the colony. Clearly there is a high degree of nest locality tenacity with 72 % of all the birds nesting within 500 metres of their nest of the previous year. Birds seldom choose the precise nest site since availability of nest sites varies from year to year due to the variable pattern of snow disappearance.

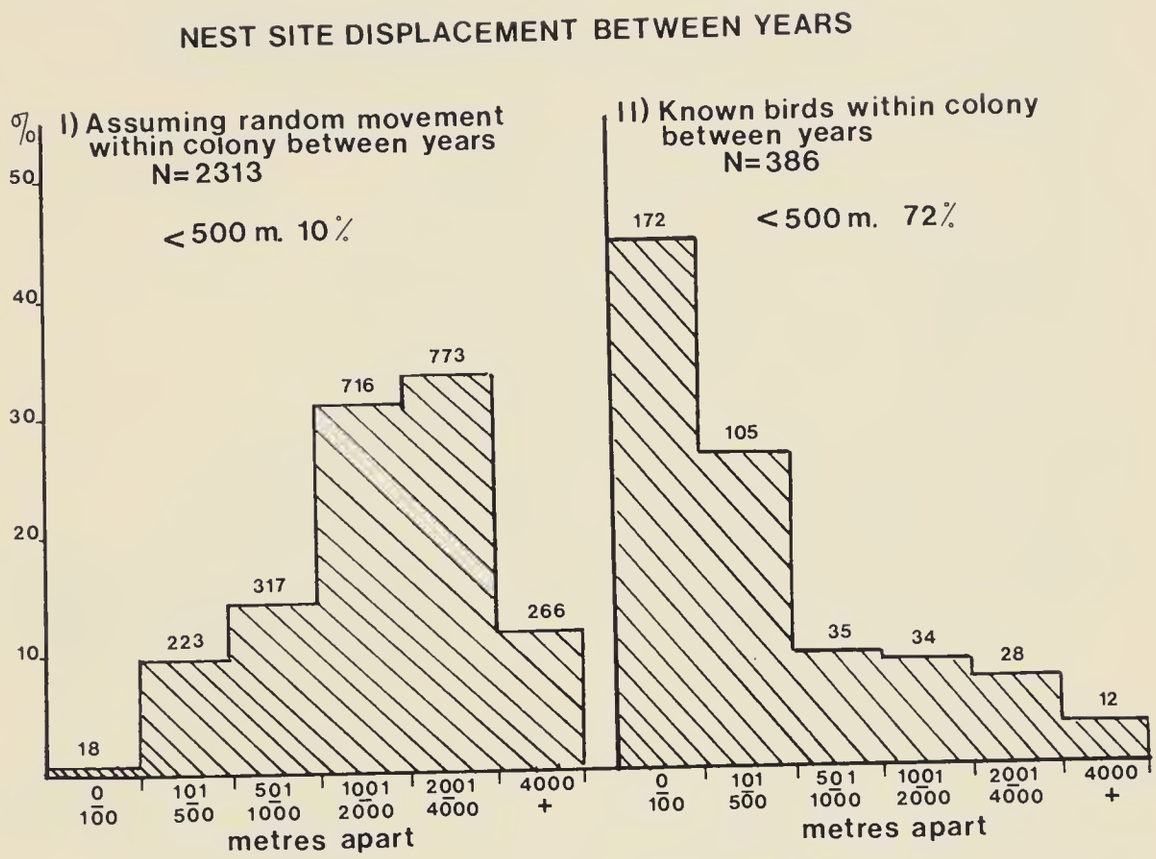

Figure 2. Nest site tenacity in Snow Geese.

One can investigate nest site displacement further. One might predict that younger birds would move nest sites more than older birds, if the first site chosen is sub-optimal and with age and experience the bird is able to find a more suitable location. Fig. 3 shows there is no evidence for this. The left histogram refers to birds banded as adults, which means that they had nested on the colony prior to the first nest used in the nest displacement data. Those which were banded as goslings include a reasonable number of first time breeders. There are no significant differences between the two histograms using a Kolmogorov-Smirnov test. Of known first breeders we have a sample of 20 birds but they too had a displacement pattern not significantly different from the adult pattern. In all cases 69—75 % of the nest displacements were less than 500 metres. Although the sample of known first breeders is small it seems to indicate that the best predictor of nest site location, at least among successful breeders, is the nest location of the first nest. Unlike the situation among some other colonial species there is no evidence of a peripheral to central shift. The pattern of location tenacity found in Snow Geese results in a patchwork arrangement of age groups on the colony. First time breeders (primarily 2 & 3 year olds) settling in a particular area will predominate in that area for several years thereafter.

The conclusion from these data is that the location of the first nest of a particular female is the best predictor of her future nest site location, but what influences her first choice?

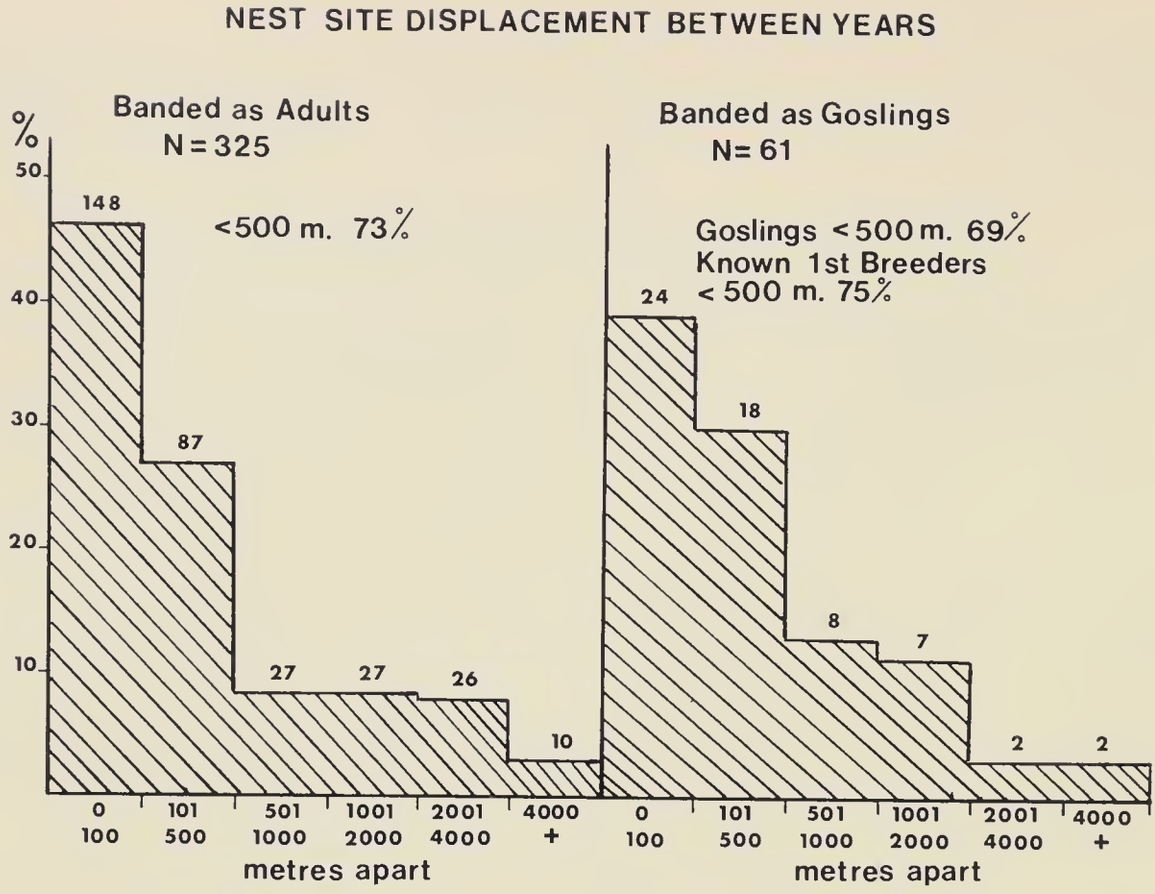

FIGURE 3. Nest site tenacity. Adults and young compared.

The pre-breeding experiences of the birds in terms of the breeding colony may influence first nest location. There are four locations used by most geese prior to breeding. These are: 1. natal nest site; 2. feeding area used by bird as gosling; 3. feeding area used by bird as yearling; 4. nest location of parents in yearling year.

Fig. 4 shows the displacement between a bird's natal nest and the location of its first observed breeding. There appears to be no difference from random movement within the colony (compare with Fig. 2). Natal nest has little, if any, influence upon the nest locality of the bird when it returns to the colony as a breeding bird.

Now we must investigate the importance of the feeding areas. As mentioned earlier we have recognized two distinct feeding areas, referred to hereafter as west and east. Banding drives take place in both of these feeding areas and despite the disturbance which the banding process entails, geese within a year remain overwhelmingly within the same area. There is also considerable tenacity to a feeding area between successive years. Only 12 % of 572 birds banded as adults were in different areas one year later. There seem therefore to be the two traditions at the colony, one for nest location, the other for feeding area. Goslings in their initial year are taken to the feeding area of their parents. Yearlings return predominantly to their natal feeding area; 87 % of 105 birds banded as goslings and resighted as yearlings were in the same feeding area. They occupy this area during the incubation period of the breeding birds but leave during hatch and moult elsewhere. Two and three year old birds, mostly first breeders, usually return also to their natal feeding areas. Of 362 birds recaptured as 2 or 3 year olds. 86 % were in the same feeding area they used as goslings. It might seem reasonable to predict that in choosing a nest location, a first time breeder seeks proximity to natal

feeding area and that this is the major way in which nest locality is influenced by earlier experience. If the natal feeding area has no influence on nest location we would expect birds from both feeding areas to be randomly distributed among the two nesting areas. This was not so and approximately 71 % of 268 birds have nested in the part of the colony closer to their natal feeding area. Natal feeding area is clearly influencing nest location but is by no means absolutely determining it.

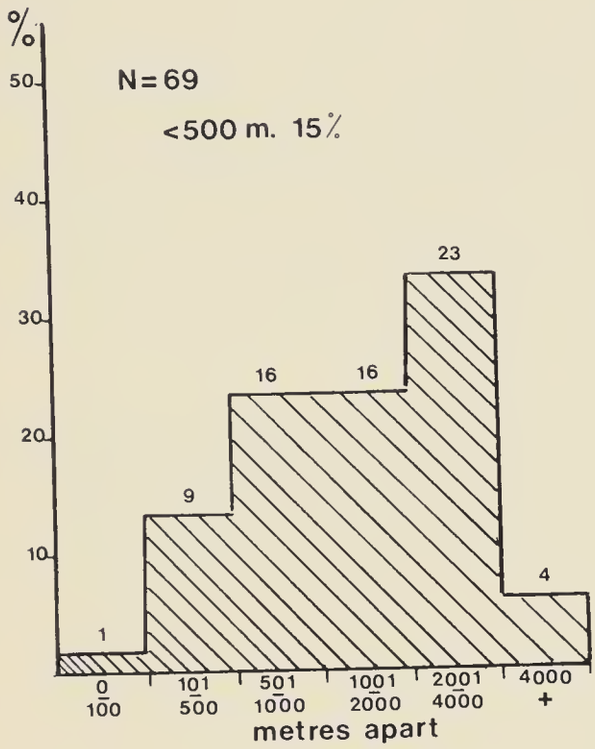

Figure 4. Relation between natal nest and nest of first observed breeding.

By looking at those birds who changed feeding area between gosling and yearling summer we get a suggestion that the nest location of the bird's parents in the yearling summer may be a factor which determines the change of feeding area. Five goslings from two families were resighted in their yearling summer in the feeding area most distant from their natal nest. In the case of both families the parents also had moved from the nest site of the gosling to a nest site in the opposite part of the colony. Among 27 yearlings whose parental nests we located in the yearling summer, all were feeding in the feeding area closest to their parents' nest of that year. Yearlings visit their parents while the latter are nesting and thus move between feeding area and parental nest site. It seems likely that this allows the birds to become familiar with the locations near to where they spend their yearling summer and to choose a nest location in that sector of the colony preferentially.

In summary it appears that the early experience affects habitat selection at a Snow Goose colony in two ways. Firstly, the feeding area used by the geese is strongly influenced by where the birds spend their gosling and yearling summers. This is determined by the bird's parents and thus a tradition is handed down from parent to offspring. Secondly, nest location is largely determined by the location of the first nest. The first nest is usually located in that part of the colony closest to the feeding area with which the bird is familiar. When a bird chooses its first nest it is concerned not only with the habitat type, with short willow being preferable to *Elymus,* but also with the proximity of

that site to a feeding area with which the bird is familiar. The nest locality seems to be strongly influenced by the feeding area tradition.

Although the general patterns of tradition seem to be established by the analysis, one is struck by the number of exceptions. Some birds move their nest considerable distances between years. Others change feeding areas. Traditions in Snow Geese are not rigid and experimentation is occurring. We would like to conclude by speculating on the potential evolutionary consequences of tradition. Some birds are highly traditional, others much less so. Let us assume that there is some genetic basis for this variation in the population. Some individuals are tradition maintainers; others are tradition breakers. We might expect some genetic variation in this behavioral spectrum in an outbreeding population. Selection under certain conditions might favor the tradition maintainers, at other times the tradition breakers. An individual which is willing to select only that habitat with which it is familiar may be at an evolutionary advantage in times of environmental stability, whereas one which is more willing to choose novel habitats may be at an advantage in time of environmental change. Some balance would be expected in the population.

To summarize anthropomorphically, geese are like humans in many ways. When choosing a home, geese are concerned not only with the quality of the real estate, nor solely with the proximity of the supermarket, they also prefer a neighbourhood which they knew when they were growing up. Also like humans, some geese are conservative and traditional, others more adventurous and radical.

Acknowledgments

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Vertical Stratification of a Neotropical Forest Bird Community

John Terborgh

Introduction

The forest environment changes in a multiplicity of ways between the floor and the top of the canopy. Not only do the physical parameters of the environment vary: higher humidity, less light, damped temperature fluctuations and reduced air circulation near the ground, as has been well documented (Allee, 1926a), but structural and biological features of the environment vary as well. Crown dimensions and crown shapes relate to position in the forest in systematic ways as do the density, orientation and diameter of stems (Richards, 1952). Light interception occurs mainly in the canopy, a fact which implies that the primary productivity of a forest is concentrated in its upper levels. This in turn suggests that the fauna of the forest floor subsists mainly on a residual economy comprised of plant parts that were not consumed in the canopy.

Taken together, these considerations point to the existence of a strong and complex gradient of conditions within the vertical reach of a forest. While this fact has not escaped the attention of biologists, neither has it received its due share of interest (Allee, 1926b; Pearson, 1971, 1975). The possibilities for adaptive specialization for the suites of physical and biological properties characteristic of different levels in the vegetational column are numerous, yet we have barely begun to explore what they are. This paper undertakes a preliminary examination of the vertical organization of a tropical forest bird community in the hope of uncovering some interpretable patterns.

Methods

My goal in the field work was to obtain a representative sample of foraging height observations for each of the 156 bird species inhabiting a 0.5 km^2 plot of submontane moist forest at 700 m elevation in the Apurimac Valley of Peru. General features of the climate, topography, vegetation and avifauna of the locality are reviewed in previous publications (Terborgh, 1971, 1977). Briefly stated, the vegetation of the plot is multistoried evergreen forest with a canopy at 30—40 m and scattered emergents to 50 m. Several streams run through the area, though they are so small as not to create any differentiated edge habitat. Only true forest interior species regularly present on the plot were included in the compilations.

The observations were accumulated over several 2—3 month visits during the period of 1968 to 1972. They cover all times of day and all weather conditions except pouring rain. My practice was to walk slowly through the forest, estimating the height of each foraging bird where it was first spotted. Subsequent estimates were made for an individual only when it moved to another tree crown (considered to represent an independent choice of foraging position). Most of the data were taken in the study plot itself, though in the cases of some uncommon or cryptic species, supplementary observations were included from nearby sites that were somewhat lower or higher in elevation. Sample sizes ranged from fewer than 10 for the most difficult species to an arbitrary maxi-

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mum of 100. Most species are represented by more than 25 observations, a sample size that has previously been shown to be adequate for such measurements (PEARSON, 1971). To facilitate further analysis, foraging height means and standard deviations were calculated for all species, although the data sets were not always normally distributed.

The analysis includes 134 out of the 156 species resident in the forest. Omitted for obvious reasons were vultures, raptors, night birds and aerial feeders. Each bird's foraging height range was arbitrarily represented by ±1 standard deviation about the mean (cf. MAY & MACARTHUR, 1972). This tactic permitted tabulations of the species using particular levels in the forest (e.g., 0, 1, 2, 5 m, etc.) and computations of the rates of species turnover between levels.

Assignments of species to guilds were based on personal observations of feeding habits supplemented with published information on stomach contents (HAVERSCHMIDT, 1968).

For comparison, a parallel set of data is included from a rainforest locality in the Cordillera Oriental of eastern Hispaniola (Dominican Republic).

Results

Dependence of foraging height range on vertical position

The range of foraging heights that may be displayed by any species is constrained within boundaries posed by the forest floor and the top of the canopy. Maximum latitude is permitted to a species that chooses a mean position in the middle tier of foliage.

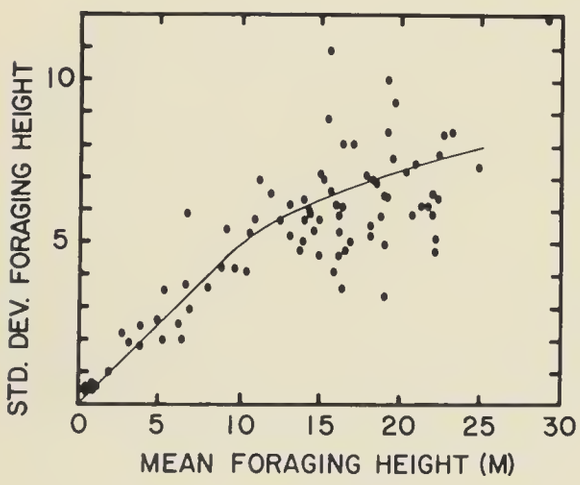

FIGURE 1. The relationship between standard deviation of foraging height and mean foraging height of birds inhabiting a tropical moist forest in the Apurimac Valley of Peru.

Whenever the preferred position is near one of the boundaries, the boundary restricts movement and effectively reduces the potential variabilitiy of behavior. This is shown in Figure 1 which gives the magnitude of foraging height standard deviations as a function of mean height above the ground. Species that live on or near the ground forage within strikingly narrow zones, which for some non-terrestrial birds may be as little as 1—2 m in depth. The same generalization should hold for obligate canopy species as well, except that (1) observations in the uppermost strata of the forest are biased downwards due to poor visibility and (2) unlike the ground, the top of the canopy is an extremely irregular surface. If instead of recording heights above the ground, I had estimated distances below the uppermost surface of the foliage, many of the species

with mean foraging heights above 20 m would have shown reduced standard deviations comparable to those of understory forms. Thus, the trend in Figure 1 should properly bow down towards the right, rather than reach a plateau as shown. This implies that species living near the ground or in the upper canopy are behaviorally specialized in the sense that they occupy narrower foraging zones on the average than do species centering their activities in the middle of the vegetational column. It can also be argued that the environment changes much more rapidly near the upper and lower boundaries than it does in between, as will be discussed later.

Overlap of foraging zones vs. height

Taking one standard deviation above and below the mean to represent each species' foraging zone, one can ask how many zones overlap at any given plane within the forest (Figure 2). The results are rather surprising. Relatively few species co-occur on the ground (17), in the understory at 2 m (13) and in the upper canopy at 30 m (12), while the mid-story at 15 m accommodates the overlap of as many as 67 species. It is unclear how this pattern relates either to the vertical distribution of foliage (concentrated near the ground) or to the vertical distribution of photosynthesis (concentrated in the canopy). These and other problems of interpretation will be considered later.

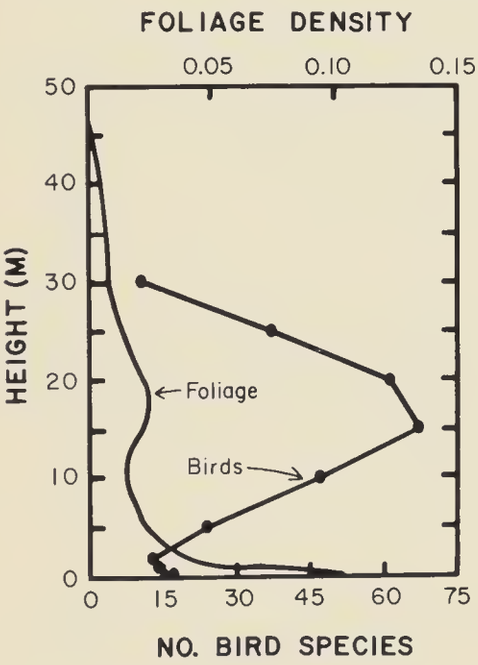

FIGURE 2. Foliage density and number of bird species vs. height in a Peruvian tropical moist forest. The number of bird species is taken as the number of overlapping foraging zones (defined as ±1 std. dev. about the mean) at a given plane in the forest.

Turnover vs. height

The fact that foraging zones are statistically (and actually) constrained near the upper and lower limiting surfaces of the forest suggests that species turnover should be greatest near these boundaries. This is shown in Figure 3. Turnover near the ground is very great indeed, reaching 74 % per m between 0 and 1 m as terrestrial species are replaced by arboreal ones. The rate falls to minimum values between 10 and 25 m and then rises toward the canopy as species drop out without being replaced. High turnover in the understory below 10 m suggests that foraging conditions may be changing rapidly within this zone, a possibility that is also implied by a sharp decrease in foliage density within the same space (Figure 2). In fact, the species turnover and foliage density curves are almost superimposable below 10 m.

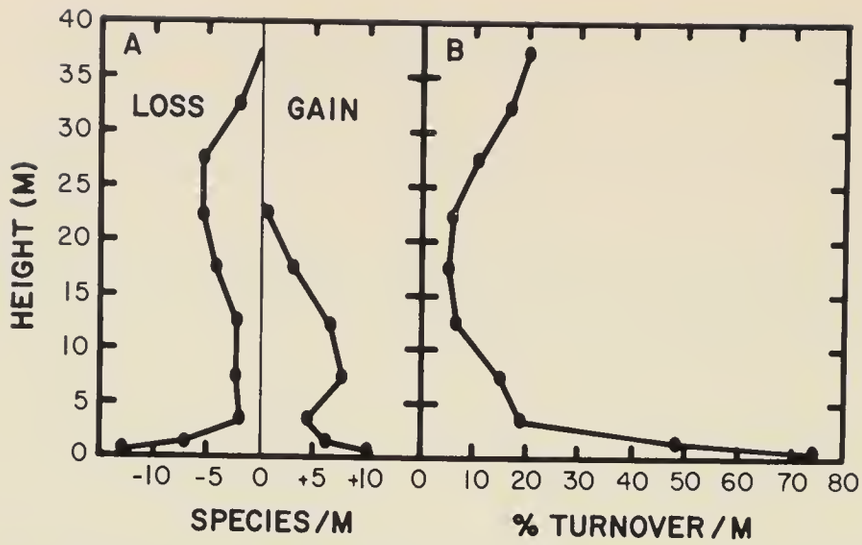

FIGURE 3. Loss, gain and turnover of bird species vs. height in a Peruvian tropical moist forest. Loss and gain are in units of species per m. Percent turnover is computed as $\frac{Li, j + Gi, j}{Ni + Nj}$, where Li, j is the number of species lost between levels i and j, Gi, j is the number gained between i and j, and Ni and Nj are the numbers of species occurring at levels i and j. All computations based on foraging height means ±1 standard deviation, as in Fig. 2.

Guild structure vs. height

That the tropical forest contains pronounced gradients both in physical conditions and in the structural characteristics of the habitat is manifestly apparent. What is not so apparent are the ways in which foraging opportunities and the availabilities of different categories of food resources may be regulated by these gradients. Direct measurements of habitat structure vs. height are notoriously laborious and have been attempted only a few times (e.g., SCHOENER & SCHOENER, 1971a, 1971b; PEARSON, 1975, 1977). Studies of the vertical distribution of food resources within tropical forests have not yet been untertaken. One can, however, attempt a rough assessment of the vertical trends in foraging opportunities and resources by using the mildly circular procedure of guild analysis. For this purpose the community is subdivided into broadly defined trophic categories. The representation in these can then be related to vertical zones within the forest (Table 1).

Several trends are evident in the results. Mast feeders occur only on the forest floor and in the canopy, while frugivores are more evenly distributed through the vegetational column. Nectarivores fall into two groups, one that lives in the understory (principally hermits—Phaethorninae) and another that forages in the canopy. Among insectivores, foliage gleaners are concentrated in the understory and canopy, while salliers prevail in between, in a reciprocal fashion. Bark gleaners forage widely up and down from mean positions near the middle of the forest. PEARSON (1975), using a different method of data presentation, noted very similar trends in his analysis of the vertical organization of three Amazonian forests.

Perhaps the most notable feature of the results is the finding that species which consume mixed diets are localized in the canopy. All species whose foraging height means lie below 10 m are dietary purists, though purists occur in the canopy as well in roughly equal numbers. Much of the increased species density in the middle and upper sections of the forest is due to the presence there of substantial numbers of dietary generalists,

TABLE 1: Peru: vertical distribution of guilds

Guild	ground	0—5	5—10	10—15	15—20	>20
			height class (m)			
Mast	3					3
Fruit	3	2	2	5	3	7
Nectar		6	2		2	1
Insects						
glean	5	10	5	2	7	2
sally	1	2	5	7	3	4
bark			1	7	4	1
Fruit/predator				1	3	1
Fruit/insects				5	9	2
Fruit/insects/nectar					4	4
No. species	12	20	15	27	35	25
No. >100 gr	6	0	0	6	6	8
Largest (gr)	3,500	35	30	1,500	520	1,050

species that feed on combinations of fruit, insects, small animal prey, or nectar. The localization of such species could be understood if the canopy presents a more coarse grained foraging environment (sensu MACARTHUR & LEVINS, 1964) than the understory, as will be duscussed later.

Comparison: Guild structure vs. height in an impoverished insular community

To determine whether the narrow foraging zones of many understory species of the Amazonian forest, and the implied high degree of specialization, are perhaps consequences of the elevated species density, I made a parallel set of observations in a structurally comparable forest in Hispaniola, West Indies (Table 2). There, with many

TABLE 2: Hispaniola: vertical distribution of guilds

Guild	ground	0—5	5—10	10—15	15—20	>20
			height class (m)			
Mast	1					1
Fruit			1			1
Nectar			2	1		
Insects						
glean			1		1	
sally			1			
bark					1	
Fruit/predator						1
Fruit/insects				2		
Fruit/insects/nectar			1			
No. species	1	0	6	3	2	3
No. >100 gr	1	0	1	0	0	3
Largest (gr)	120	0	102	75	34	ca 450

fewer species (15 vs. 134 in Peru), the pattern obtained is similar in the vertical distribution of dietary guilds (e.g., mast eaters on the ground and in the canopy, frugivores well distributed, etc) but differs strikingly (1) in the complete absence of species narrowly adapted to the understory and (2) in the concentrations of foraging height means in the lower-middle portion of the forest between 5 and 15 m. A focusing, rather than a dispersion of foraging zones can be viewed as an adjustment to a low density of potential competitors. Each species, here virtually alone in its guild, is free to exploit the vegetation as widely as it can within limits imposed only by the interaction of its morphology with the habitat gradient.

Size vs. height

One way in which morphology seems clearly to interact with habitat is in the matter of size. In both Peru and Hispaniola large species (arbitrarily weighing >100 g) are confined to the forest floor and canopy, as Pearson (1971) also observed at his Peruian site. The only exception is a 102 g cuckoo *(Saurothera)* which adheres to the common pattern for Hispaniolan species of centering its foraging in the 5—10 m zone, where the lizards it preys upon may be maximally abundant (Schoener & Schoener, 1971a).

The bimodal occurrence of large species could plausibly relate either to the distribution of suitably resilient perches (scarce in the spindly shrubs and trees of the understory) or of resources (e.g., large fruits are produced mainly in the canopy). Resolution of the matter awaits the measurement of vertical resource profiles in tropical forests.

Discussion

Guild representation vs. the vertical habitat gradient

It seems reasonable to infer that the uneven representation of guilds with height in the Amazonian forest mirrors an underlying unevenness of foraging opportunities and resource availabilities. Some examples serve to illustrate the point. Mast seems to be available only on the ground after it has fallen, or in the tall trees which produce it. The smaller trees that fill in the middle of the forest produce quantities of soft fruits, but not mast, as judged by the infrequency with which one observes large parrots beneath the canopy.

Dense foliage near the ground provides continuous foraging substrate that is best exploited by gleaners, while the greater visibility offered by the more open middle section of the forest is advantageous to salliers. Gleaning is favored in the canopy, because the huge crowns again offer broad continuous expanses of substrate.

It is the large size of canopy crowns that also seems to offer the best explanation for the concentration of mixed feeders in this stratum. One tree may offer good insect foraging, another fruit, a third nectar, etc., but good trees for any one of these resources may be tens or hundreds of meters apart. A bird which occupies a territory of only a few hectares would do better as a dietary generalist in such a patchy environment, as predicted a number of years ago by MacArthur & Pianka (1966). In contrast, the understory is far more homogeneous. Not only is there a greater density of foliage, with fewer gaps, but the individual crowns are small and closely spaced. Many understory plant species are consequently much more abundant than canopy trees which

commonly grow at densities of only a few individuals per km^2. Hence it seems probable that the understory offers more evenly dispersed resources that are most efficiently harvested by specialists.

Turnover, species density and the habitat gradient

An unexplained feature of the results is the finding that the middle level of the forest accommodates many more species than either the ground or the top of the canopy. While a thorough analysis of this pattern would involve a great deal of research, it may be possible, in a speculative way, to anticipate some of the underlying causes. Heterogeneity of the substrate is one important consideration. The forest floor, for example, is structurally simple and uniform. It supports a collection of fruit and mast eaters that differ markedly from one another in size, and an assortment of insectivores that (1) peck insects from the surface of the leaf litter, (2) turn over the leaf litter to uncover hidden prey, (3) flutter up to snatch insects from the undersurfaces of leaves, or (4) search the dark recesses of brush piles and of fallen logs. It is hard to think of many more functions that could be performed on a two-dimensional substrate.

The above ground portions of the forest offer a much greater array of possibilities. Substrates include leaves, branches, bark, dead wood, epiphytes, termite nests, and caches of dead leaves and debris; in addition there are both horizontal and vertical perches separated by open space in which to capture flying insects. Quite simply, there are more kinds of profitable operations that can be performed in a complex three-dimensional environment.

Finally, at the top of the forest the habitat again assumes a two-dimensional character. Branch diameters narrow, the availability of vines, rotten wood, epiphytes and dead leaves declines, and foliage density increases, restricting the variety of sites used by sally feeders. Bird species diversity falls concomitantly, presumably in response to the reduced array of foraging opportunities.

Another aspect of the problem, one that may have interesting theoretical implications, concerns the fact that species' foraging zones are broader in the midsection of the forest than in the understory, and probably high canopy. A species which forages exclusively in a band 1—2 m deep will maintain a larger competitive presence within its foraging zone than will a species which uses a band that is 15—20 m deep. It may be that the more concentrated foraging zones of understory species effectively amplify competitive interactions so that coexistence is reduced below the levels attained in the middle and upper tiers of the forest.

Turnover vs. heights

My final point concerns the high rate of species turnover in the understory. The turnover is of course due to the narrow foraging zones of the species inhabiting this portion of the forest, and these seem clearly to be the result of specialization. This is brought out in the comparison with the Hispaniolan bird community. The understory is no less used (as judged by the frequency of observations and mist netting), but it is used by species with much deeper foraging zones centered in the middle portion of the forest. While it is not surprising that a species poor insular community contains no specialists, the question posed by the Amazonian community is: what is there about the

understory that permits such finely tuned specializations to evolve? My feeling is that the answer lies in the organization of the vegetation.

At least three structural features of the understory environment may contribute to the possibilities for specialization. One is the close juxtaposition of distinct strata. Of the five layers recognized by RICHARDS (1952) as characteristic of the tropical rainforest, the lower three (C, D and E), are crowded into the bottom 10 m of the forest, while the upper two (A and B) fill the upper 30 to 50 m to the tops of the tallest crowns. Strata thus become progressively more telescoped closer to the ground. This results in a sharp gradient of foliage density in the understory, as shown in Fig. 2. And lastly, associated with the high density of foliage and turnover of strata, are additional gradients in mean stem diameter and stem orientation. It is only within two meters of the ground, for example, where the density of slender vertical stems is very great, that one finds species (other than trunk feeders) which characteristically perch on vertical stems. Though the connection in this case is obvious, there are undoubtedly additional explanations for the restricted vertical foraging zones of understory species.

Acknowledgment

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Evolution of Habitat Use: Geographic Perspectives

Martin L. Cody

Introduction

The title of this symposium presents us with a considerable challenge since, while we know a good deal of the controlling factors in habitat selection and use, and something of the mechanism of the choices involved, we know as yet very little about the evolution of these traits. Evolution affects gene frequencies which are population characteristics, and my contribution therefore emphasizes a comparative and geographic approach among ecologically related bird populations and communities. However, most of the facts I present are more a description of the outcome of selection for differential habitat use than an evaluation of the forces that have produced this outcome. Such a bias seems unavoidable in view of our ignorance of the evolutionary aspects, but I hope at least to identify variations over some broader aspects of space and time that may lead us to appreciate the evolutionary questions.

In the three sections below I discuss firstly a useful methodology for describing habitat utilization in the familiar terms of bird density and diversity, such that strictly quantitative comparisons between populations are possible. Then I describe the complementary approach from community studies, by asking whether the consequences of broad versus narrow habitat utilization by bird populations are apparent from the structure or organization of their communities. Thirdly, I compare habitat use in geographically distinct warbler communities that differ, in particular, in their ages, the geologic time spans over which the species sets have likely been associated within a given habitat range.

Description and comparison of habitat utilization

Within a reasonably circumscribed region a species is found in certain habitats and not in others; we need a quantitative description of this selectivity. My approach (see Cody, 1975) has been to rank or ordinate the habitat types into a habitat gradient H, such that a species is absent over some lower H values, occurs with increasing density to peak at an intermediate value on H, and thence decreases in density to finally disappear at higher H values. Thus the density distribution U (for use or utilization) of species i, U_i (H), is a unimodal monotonic curve over H. A description of the habitat use of the species comes from two parameters of this curve, one a measure of the position of its peak on H and the other a measure of its spread or variance over H. Relatively simple habitat ordinations, such as those based primarily on vegetation height, serve to produce similar unimodal curves in most of the species that occur on the habitat gradient. Thus as one moves from lower to higher H values (e.g. through vegetation of increasing height) earlier occurring species are lost while new species are gained, themselves to be lost later in favor of other species that are distributed over still higher H values.

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The process of continual loss and gain of species over the habitat gradient is described by a species gain curve g (H) and a species loss curve l (H), which become gain and loss rates if the curves are linear. We can immediately define α-diversity as [g−l], the way in which species packing levels vary with H, and β-diversity as ½ d/dH [g+l], the rate at which new species replace old species as one moves over the gradient H. This last statistic describes the relative habitat utilization of the bird populations over habitat types; it is the habitat specificity component of bird diversity, and is potentially independent of α-diversity.

An example of the application of these techniques is given in Fig. 1. Here I show the α-diversity and β-diversity curves of four matched habitat gradients in the Mediterranean-climate regions of four continents: southern California, central Chile, southern Sardinia and the Cape Province of South Africa. For these four areas the species gain- and loss-curves are best fit by sigmoid curves, and so the α-diversity curves are also sig-

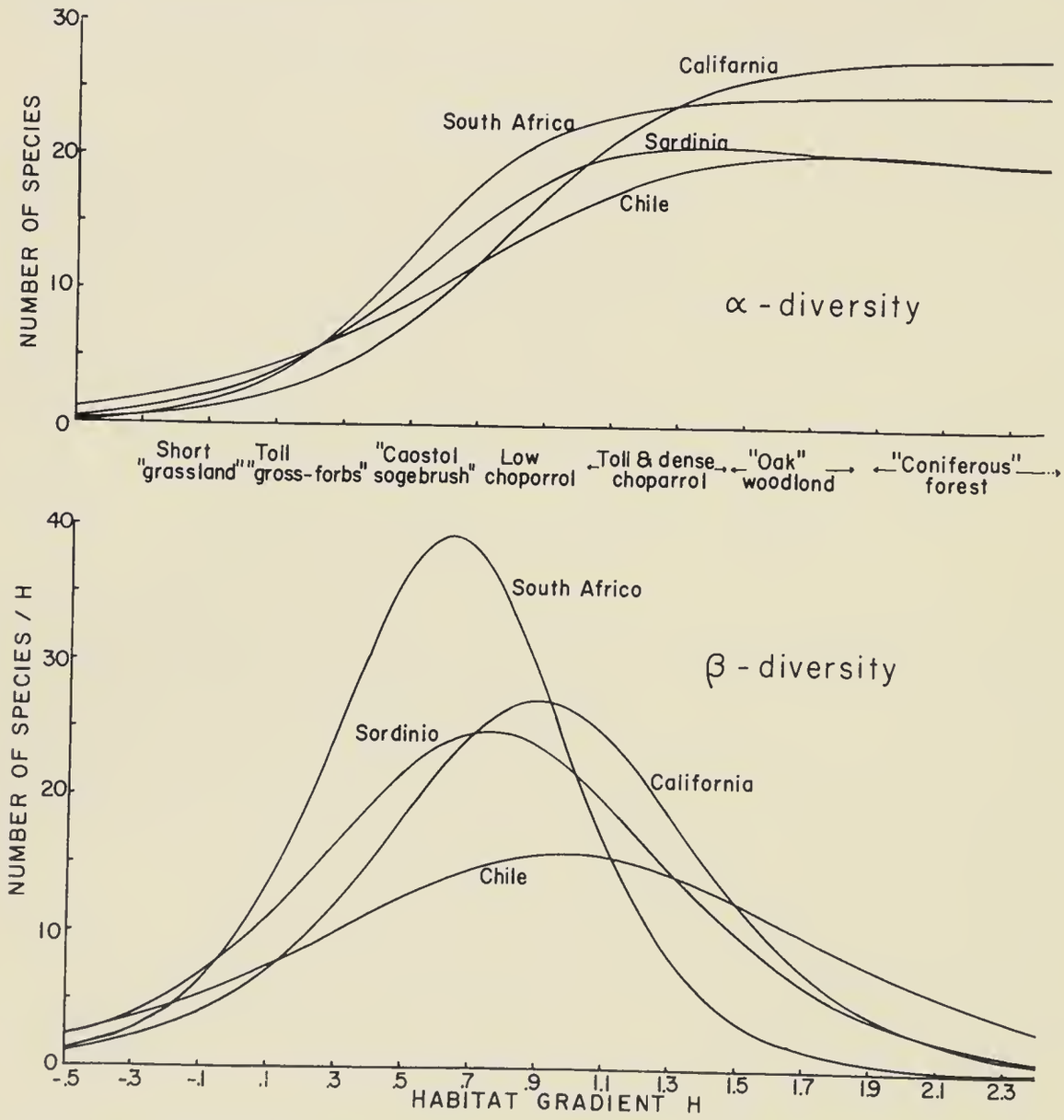

FIGURE 1. Diversity curves for regions on four continents with comparable Mediterranean-type climates. (a) above: curves of α-diversity, showing increasing numbers of (breeding) bird species with vegetation height from left to right across the habitat gradient. (b) below: curves of β-diversity, the rate at which species turnovers occur per unit habitat change, show far less similarity among continents than do the α-diversity curves.

moid; these curves are relatively similar in each of the four sites. The β-diversity curves, on the other hand, are quite different from each other, indicating that the extent to which bird species use the (same) habitat gradient differs considerably, both among continents at a given point on the habitat gradient and between different habitats within a region. In particular, β-diversity is lowest in Chile and highest in South Africa over most of the habitat gradient, but is high in California and Chile in taller habitats.

In Fig. 2 I redraw the diversity curves in one plane that is divided radially to correspond to divisions along the habitat gradient H. In an effort to interpret the distinct curves in the diversity plane, I have looked at the frequency distribution of habitat itself over H, and the total areas of "accessible habitat" in the four regions under consideration (see Cody, 1975, in part). I find that this information goes a considerable way towards explaining the patterns in Fig. 2. For example, although α-diversity is largely determined by habitat structure (H) and is relatively invariant among continents, α-diversity is boosted in those habitats where β-diversity is high. In turn β-diversity is greatest on that part of the habitat gradient where the areal extent of the habitat is highest, and the total number of species censused over H, related to the area under the β-diversity curve, bears a close relation to the total area of accessible habitat for the region.

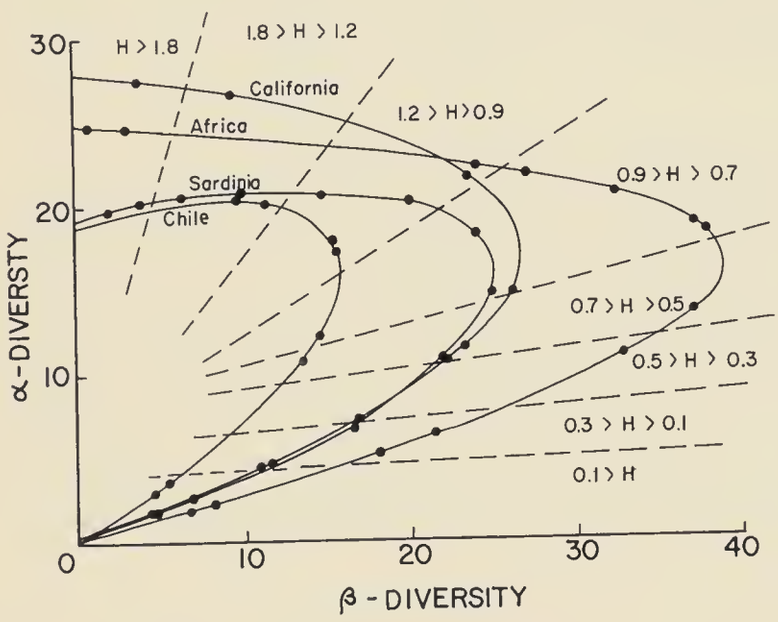

Figure 2. Diversity curves for four Mediterranean-climate regions. The extent to which curves differ is most apparent on the abscissa, which measures relative habitat utilization. Rules for deriving these curves a priori from a knowledge of the relative and absolute frequencies of habitat types are contemplated (see text).

The curves in Fig. 2 are three-parameter curves, and there are three sets of rules which determine these parameters: (a) rules for α-diversity primarily as a function of H and secondarily as a function of β-diversity; (b) rules that determine β-diversity as a function of both relative and absolute areal extent of habitat at H; and (c) rules that describe the total species complement of a region in terms of accessible habitat or source area (Cody, MS). While these notions are not developed here, it is hoped that eventually they will contribute to a theory of continental species diversity and in particular to its most variable component, habitat utilization.

Habitat use and community structure

The question as to whether differences in relative habitat utilization on a habitat gradient are reflected in community organization is next asked: Is the fact that South Afri-

can birds show a much higher β-diversity than average and Chilean birds show a much lower β-diversity revealed in local community studies? A detailed analysis of tall macchia habitats, at a value around H = 1.0 on the habitat gradient, was recently completed (Cody & Mooney, 1979) in matched 2-ha sites on each of the four continents.

Looking firstly at the morphological attributes of the breeding bird species, principal component analysis shows that both the means and the variances of the first two axes of variation are not statistically different among continents. Likewise, a similar analysis of the foraging behavior and foraging height distributions brings to light no differences among continents; not only is the composition of the principal component variables similar in all cases, but similar amounts of the total variation in each site are accounted for by each variable.

I then ask, using canonical correlation analysis, if bird morphology is similarly related to foraging ecology on each continent. The answer is affirmative, apart from a tendency for the Chilean habitat generalists to be larger-bodied than their counterparts elsewhere, and a detectable tendency for more overlap in foraging height distributions among the South African habitat specialists. The four continents show similar axes of morphological and ecological variation at the macchia sites, and these axes are related to each other in very similar ways. Thus community organization at the detailed resolution of 2-ha sites gives very few clues to the differences in broader patterns of habitat use that appear by analysis of distributions over gradients.

Habitat utilization in *Sylvia* warbler communities

I have studied habitat selection and community organization in warbler communities in four main regions: the High Atlas of Morocco, southern Sardinia, northern England, and southern Sweden (Skåne and Öland). In each region I located *Sylvia* territories and measured the structural characteristics of the vegetation in each; the sample sizes are comparable, with 116 territories in Morocco, 150 in Sardinia, 79 in England and 92 in Sweden (Cody, 1978, 1979 and MS; Cody & Walter, 1976). From the measurements of vegetation structure I derive the linear discriminant function that best segregates species at each site; in every case 85 %—90 % of all interspecific segregation by habitat is displayed in this new habitat variable.

Fig. 3 shows the warbler distributions over this discriminant function. Apart from the fact that there are more species in the High Atlas (7) than in England or Sweden (5), the habitat utilization curves differ considerably among sites. In Sweden all species are common over broad ranges of habitat with plenty of overlap among species. In fact *S. nisoria*'s (N) preferred habitat is local in southern Sweden, and in England the habitat of *S. undata* (U) is similarly restricted to the south coast. The other four English species again show broad habitat use and extensive interspecific overlap, but here they segregate into two groups, with *communis-curruca* in lower habitat and *borin-atricapilla* in taller habitat.

The Sardinian species show in general a more discrete habitat segregation, with two exceptions: the centrally positioned *melanocephala* (M) encompasses the habitats of four more specialized species, and two of these, *conspicillata* (CON) and *sarda* (S), live in structurally similar habitat with the former in coastal areas and the latter on mountainsides. The situation in the High Atlas is more confusing. Only four of the seven

species are common wherever their habitat is found (*deserticola* D, *melanocephala* M, *cantillans* C and *atricapilla* A), and these four show broad habitat overlaps. Of the other three species, *undata* (U) is rare and very patchily distributed over a range of habitat, *communis* (COM) is a strict habitat specialist although not uncommon where its scarce habitat is found, and *hortensis* is so rare that little can be said of its status or preferred habitat. In fact the High Atlas supports only a subset of the 9 Moroccan *Sylvia* species, since U and H are common and D much rarer in the northerly Rif and Middle Atlas Mts, *conspicillata* is common in *communis* hatitat in coastal and northwestern plains, and *nana* occurs only in the desert. At the other three sites the *Sylvia* species found are those of the country as a whole.

I suggest that the differences in habitat utilization among the four sites in latitudinal sequence are related to putative differences in age between communities (CODY, 1979), with the older communities in Morocco and the younger communities in which the species have been together only a few thousand years in the north. The patterns of

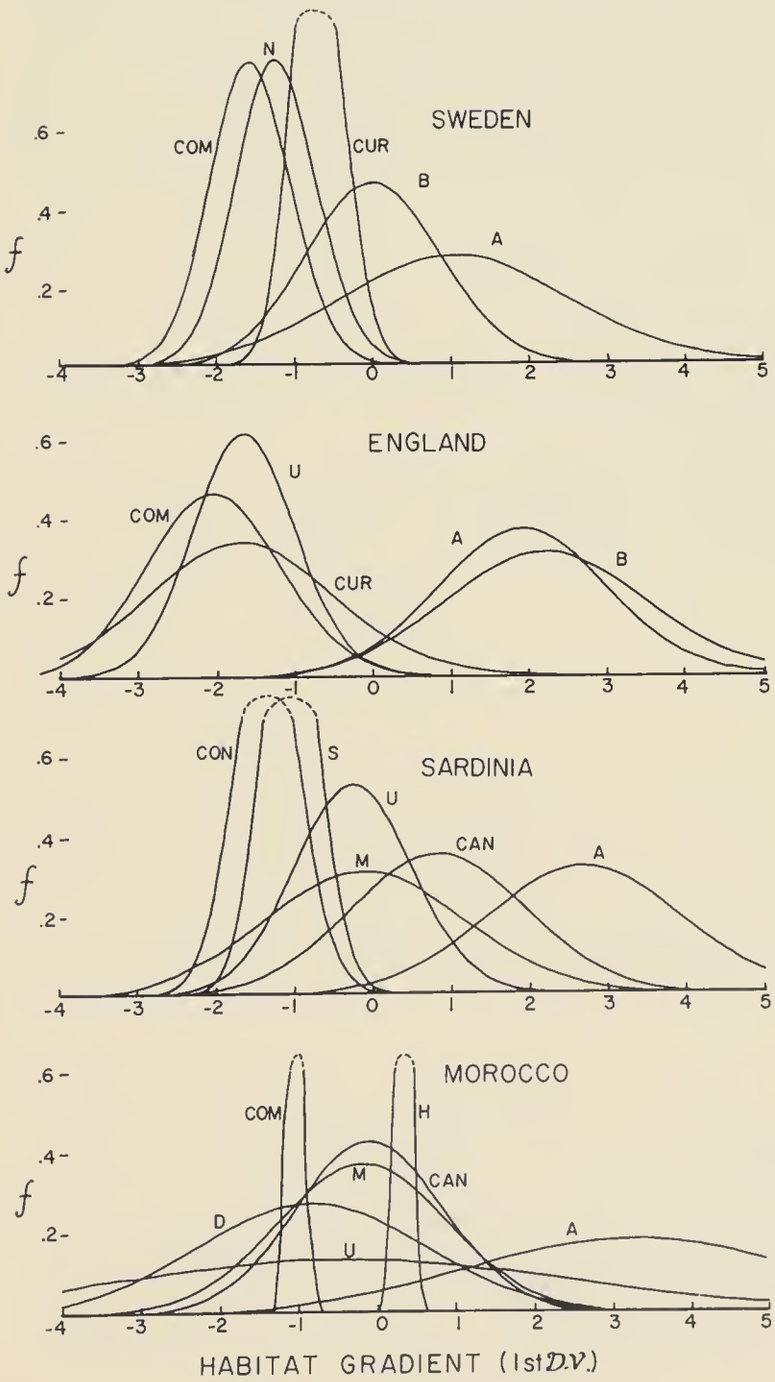

FIGURE 3. Distribution of *Sylvia* species over a discriminant function rendition of habitat gradient at four sites in a latitudinal sequence. All curves are unit-area Gaussian frequency distributions. The data are derived from analysis of 80—150 territories in local areas of each country named (see text). The *Sylvia* species represented are: A: *atricapilla;* B: *borin;* CAN: *cantillans;* COM: *communis;* CON: *conspicillata;* CUR: *curruca;* D: *deserticola;* H: *hortensis;* M: *melancocephala;* N: *nisoria;* S: *sarda;* U: *undata.*

habitat use can give an evolutionary perspective only by consideration of further information on interspecific interactions. There is a clear trend from north to south in the extent to which direct competition affects territory choice. I have measured complete and partial interspecific territoriality, allospecific fights, chases and reactions to song playbacks; these phenomena are common and general in Sweden, more stylized and restricted (e.g. symmetrical interactions with song convergence) in England and Sardinia, and are not seen at all in Morocco. The broad overlaps in habitat preference among the Swedish species do not reflect that habitat occupancy is severely restricted by direct competition from other species, whereas broad habitat overlap among Moroccan species, which do not directly interact, is indicative of territorial co-occupancy by several species with different foraging ecologies.

The evolutionary trend in habitat selection in this genus can be hypothesized as follows: initially there is broad overlap among habitat generalists with similar foraging ecologies but territory use is regulated through direct interspecific interaction; thence a more conventionalized and less overt direct competition occurs with increasing habitat segregation, leading eventually to local allopatry together with the coexistence of both habitat specialists and habitat generalists with territory overlap facilitated by differences in foraging ecology. Further studies on *Sylvia* communities and on comparable groups that can provide both geographic and time perspectives are needed before further speculation is justified.

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Seasonal Changes in the Use of Avian Habitat in Southern Africa

Richard Liversidge

This paper reviews how the avifauna of the semi-desert habitat of the Kalahari National Park, South Africa, changes in the course of a year, and varies between successive years as living conditions fluctuate in response to rainfall. Arid zone birds, living in areas where the conventional concept of habitat as an area supplying all the species needs does not apply (see the review of Hilden, 1965), differ in basic ways from those inhabiting better-watered and more predictable habitats. The bulk of desert birds are nomadic (MacLean, 1974), an adaptation that allows the individual to move about to find suitable conditions for breeding. Arid zone birds do not necessarily breed every year (Immelman, 1963; MacLean, 1970b), and they are subject to unusual physiological stress factors associated with thermo-regulation and water metabolism.

The present study was carried out during the years 1974—1977. The average annual rainfall varied considerably during this time (532 mm in 1974, 234 mm in 1975, 602 mm in 1976, and 263 in 1977), in two of the years being three times the mean annual figure of 200 mm (35-year average). Visits were made to the area during the survey at approximately 4 month intervals. On each visit a 580 km strip census was completed, 330 in riverine habitat and 250 in dune habitat. For definitions of these habitats see Leistner (1967). The dry river beds with large camel thorn trees are favoured by many birds that would otherwise not be considered typical of the Kalahari. To better determine habitat utilization in relation to feeding requirements the species have been broken into the following groups: Ostrich, Raptors, Insectivores, Mixed feeders and Seedeaters. The counts are expressed as numbers of birds seen per 100 kilometres. The strip count covered 100 metre width for passerines in the dunes and twice that in riverine habitat, 400 metres for non-passerines except Ostriches and Raptors where 1000 metres in riverine habitat and 2000 metres in dunes were taken in. Fig. 1 illustrates the population changes during the period relative to rainfall.

Ostrich *Struthio camelus*

This species shows a seasonal cycle of abundance which increases during the main summer rainfall period. It is suggested that the increase is linked to improved grazing conditions which are dependent upon rainfall. As both Sauer (1964) and MacLean (1974) point out, Ostriches may breed throughout the year, but there is a peak of breeding at the beginning of the rains. The increase in numbers is not sufficiently early in the rains to indicate a move into the area for breeding purposes only.

Raptors

This group is dominated by the Secretary Bird *Sagittarius serpentarius,* Vultures *Gyps africanus* etc., Tawny Eagle *Aquila rapax,* Chanting Goshawk *Melierax canorus,* and various other large eagles. Raptors show a similar cycle to the Ostrich. The numeral increase in summer is in part due to native species, including the new offspring of resi-

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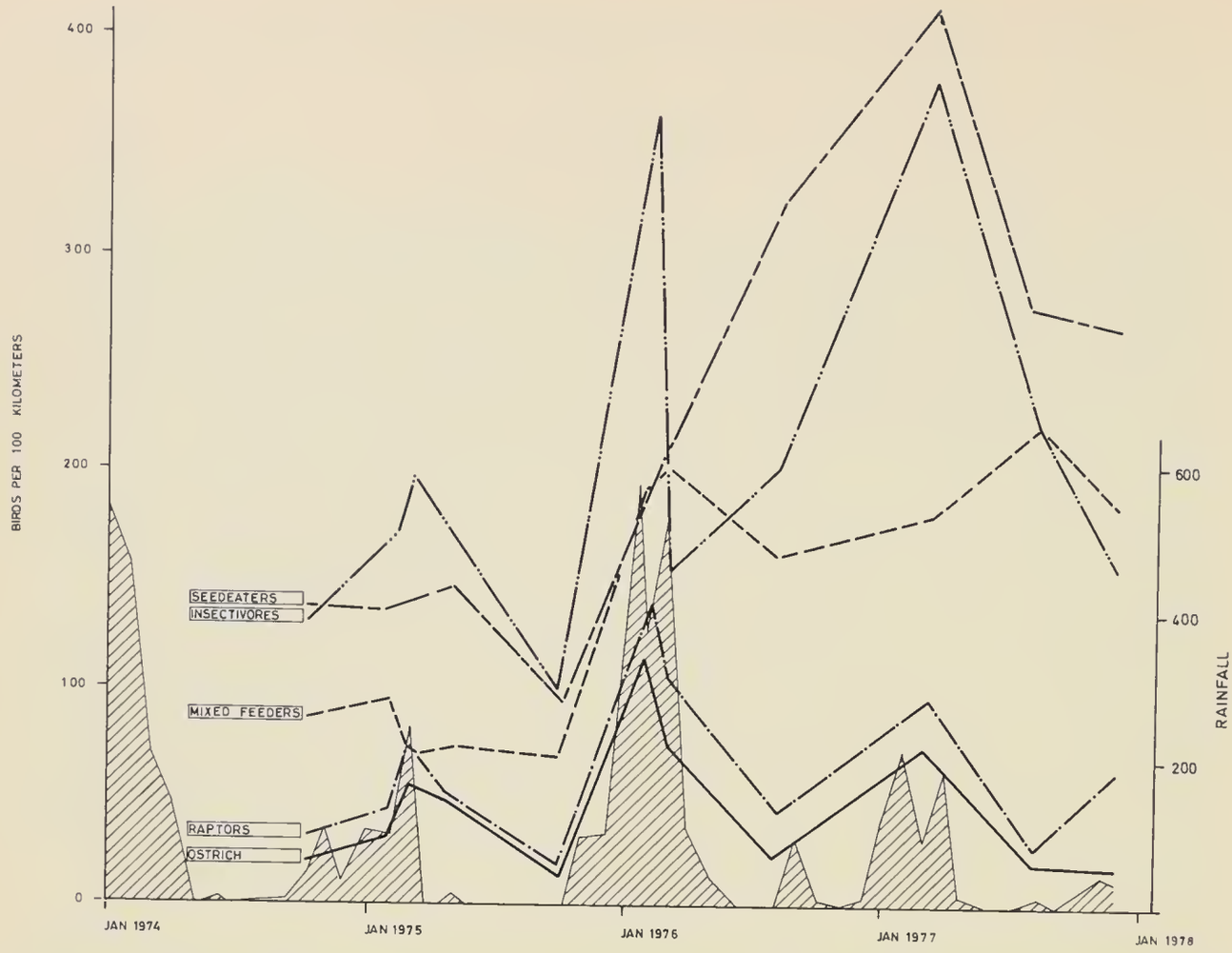

FIGURE 1. Bird population levels in the Kalahari National Park (numbers counted per 100 km) and rainfall.

dent species, and in large part to the migrants from Europe and Central Africa. However, the increase due to migrants is not as great in the Kalahari as RUDEBECK (1957) suggests for elsewhere in southern Africa. It may be noted that the endemic Martial Eagle *Polemaetus bellicosus* is virtually absent in summer, whilst the Bateleur *Terathopius ecaudatus,* also endemic, is far more numerous in summer, when it breeds.

Insectivores

Dominant species are Kori Bustard *Otis kori,* Crowned Plover *Stephanibyx coronatus,* Swallow-tailed Bee-eater *Dicrocercus hirundineus,* Lilac-breasted Roller *Coracias caudata,* Fork-tailed Drongo *Dicrurus adsimilis,* Chat Flycatcher *Bradornis infuscatus,* shrikes *Lanius collaris* and *minor,* and Cape Glossy Starling *Lamprotornis nitens.*

The populations increased dramatically in mid-summer each year. In winter 1975 the drop-off in numbers was considerable, probably because previous years had been so dry. The decrease in the winter of 1976 was not so great, and in 1977 there was only a gradual decline in numbers through winter to midsummer. The summer populations of 1977 were greater than the previous year although the rainfall was far less. Figure 1 shows that there was a carry-over effect of the high population probably due to an abundant food supply from the previous good year. Populations of passerine insectivores decreased in winter more than those non-passerines.

Seedeaters

Dominant species are sandgrouse, esp. *Pterocles namaqua,* doves *Streptopelia capicola* and *Oena capensis,* Finch-larks *Eremopterix verticalis,* sparrows *Passer diffusus* and *melanurus,* and Scaly-feathered Finches *Sporopipes squamifrons.* Figure 1 shows that there was a delayed numerical peak in late summer after the peak rainfall period. This is presumably because it takes many weeks for seeds to be produced after rain. Furthermore after the good rains of 1976 there was no winter drop, but a steady build-up of numbers through the winter until the following summer. This shows the remarkable carry-over effect of the food supply for this group. Passerine and non-passerine seedeaters showed the same fluctuations.

Mixed feeders

Dominant species are the Larks *Mirafra africanoides, M. apiata,* and *Certhilauda albofasciata,* Sparrow Weavers *Plocepasser mahali,* and Social Weaver *Philetairus socius.* There was a distinct summer peak. Total numbers showed a considerable increase in 1976 which continued through into 1977, showing that the carry-over effect found both in insectivores and seedeaters is applicable to the group.

Total bird populations

The summer population varied from 731 birds to 1739 birds per 100 kilometres. Using these figures and distance of visibility it is possible to estimate population. Over the four years the mean population was roughly 33.2 birds per hectare for the riverine habitat and 24.9 birds in the dunes. It is interesting to note that ERZ (1966) gives a figure of 25.4 birds per hectare for rural Europe. It should be noted that fortuitously the rainfall recorded over the period of study was the heaviest since records were maintained (35 years) and conditions better than living memory could recall. In MACLEAN's work (1970b) over 19 months during a very dry period it is understandable that there would be different conclusions. Thus he states (1974) that nomadic birds are predominantly granivorous. Whilst Figure 1 shows that this was so in this study in 1977, in 1976 insectivores (especially Wattled Starlings *Creatophora cinerea*) were more numerous. This whole question throws doubt upon the conclusion of PIANKA & HUEY (1971) who compare differences between Australian and Kalahari desert conditions based upon one year's work in the Kalahari. With population fluctuations of the magnitude of 2.4 in four good years we can expect a greater variation compared to dry years; thus one year's results are to be treated with caution. They state for example that arboreal birds are added faster than ground birds as species density increases. This ignores MACLEAN's comments (1970a) that sometimes many thousands of nomads (especially larks) move into an area from one day to the next. My own observations would fully support MACLEAN in this matter.

It is important that studies of this nature should be relatively long term to include both dry and wet periods. The indications are that the dry periods favour seedeating species whilst extreme wet periods favour insectivores. In a short term research project in the semi-arid Kimberley area, CROWE (pers. comm.) found a direct correlation between rainfall and biomass of seed and arthropods. But our knowledge of biomass of food is lacking. This is especially true of the carry-over effect which we can only guess

at from the avian population figures obtained. A rodent research project run simultaneously in the same area (NEL, 1978) shows that the rodent population does not peak at the same summer rainfall periods as the birds do. The rodent population numbers are greater in the dryer years than in the wetter years. It is evident that the rodent populations and seedeating bird populations are not controlled by the same factors, since the rodent populations peak, roughly speaking, at 24 month intervals.

Nomadic species

As has been mentioned by MACLEAN (1970b, 1974) and others the nomadic species are numerically the most abundant in the Kalahari. These include primarily various species of larks Alaudidae, and seedeaters Ploceidae and Fringillidae, to which must be added the Wattled Starling, sandgrouse Pteroclidae, and the doves Columbidae. The last three are capable of powerful flight and can cover considerable distances. It is therefore not surprising that these are able to find suitable habitats. The smaller passerines are not such good flyers; moreover they usually do not fly at the same altitude as species mentioned above. It is assumed from the fact that species are some years abundant, and some years entirely absent from various parts of our arid regions, that these populations move around and in this way seek out favourable habitats. Thus if good rains have fallen in Namaqualand there are large numbers of seedeaters and larks as well as sandgrouse and Namaqua doves present. The subsequent year might find very few birds in that area but a sudden influx perhaps 500 kilometres away in the Kalahari or southern Namibia. In effect these birds are seeking out the suitable habitat where they can remain either as non-breeding birds or as breeders depending to an extent on the time of year. As IMMELMAN and MACLEAN have shown, these desert nomadic species are able to breed at almost any time of the year although there is normally a summer rainfall peak period.

Nomads presumably seek out a habitat which will meet their minimum requirements. An area suitable one year may not be acceptable the following one. This forces the birds to move on until the desired conditions have been satisfied. Within this generalised area proximal factors will influence the birds' actual habitat selection and residential area. MACLEAN (1970b) comments that these thousands of nomadics may "move into an area from one day to the next and they may disappear just as suddenly".

The social nomadic behaviour of such numerically abundant birds as sandgrouse, doves, Wattled Starlings, certain larks, sparrows, weavers, finches and buntings is adapted to these harsh and often different local habitats. Their movements must be rapid during the search for suitable habitat because the hostile conditions that pertain could not support large numbers for long. They are compelled to move until the ecological minima are reached. Taking into consideration the many and varied species of birds involved the area over which such a search can occur must be enormous in extent. This area is available in southern Africa through the regions known as the Karoo, Kalahari, Namaqualand and the Namib. Each is vast in itself and liable to provide at one end or another suitably good conditions. That each area borders two or three of the others allows adequate reserves for the species to survive. This phenomenon has been sketched for Australia (KEAST, 1960; IMMELMAN, 1963, 1966) where 30 % of the avifauna is nomadic. This is far greater than for southern Africa where a large portion of

our species are migrants either wihtin Africa or intercontinental. Probably less than 20 % of endemics are nomadic.

Discussion

The above facts and figures illustrate clearly that the same habitat is utilized to a different degree from year to year. The unpredictability of the desert environment and the varied adaptive responses of birds to it suggest that it would be revealing to interpret the latter in terms of the ultimate factor and proximate factor concept of JOHN R. BAKER. Ultimate factors were seen as those factors that, in the evolution of the species, had programmed it to breed at the optimum time (e.g. spring) and to seek certain attributes in the breeding site (i.e. those that would optimise its success). Proximate factors, on the other hand, are those involved in immediate responses, e.g. rainfall as a trigger to breeding or migrating. In the desert situation, obviously, the distinction is less clear-cut than in normal areas; nevertheless the two can still be distinguished. In the Kalahari "ultimate" factors could be thought of as influencing the annual settlement patterns of nomadic species in particular, but would also influence the non-breeding migratory species which come into the area for their winter quarters. The ultimate factors are thus those that concern the species as a whole, and are not of particular importance so far as the immediate onset of breeding is concerned.

HILDEN states the basic ultimate factor is food. In semi-desert or arid situations it is suggested here that food is directly proportional to rainfall, so the emphasis should be placed on rain as much as food for arid conditions. Rainfall brings an immediate increase in insect life, leaf production and, ultimately, seed production; indeed it changes the whole environment almost immediately. In some parts of the world desert birds react to rain almost immediately (IMMELMAN, 1963, 1970). The response is not so dramatic in southern Africa for most species. However, the resident *Plocepasser* started carrying nesting material with the first fall of rains. Nomadic species such as *Sporopipes* and *Fringillaria impetuani* started breeding within a week even though it was not the usual breeding period (see also MACLEAN, 1974). Rainfall is thus both a proximate and an ultimate factor.

A further ultimate factor is "shelter from enemy and climate". It is felt that the latter is the second most important ultimate factor for desert species—see DAWSON (1976), who discusses the problems desert birds experience in thermo-regulation and water metabolism and how these are met by special adaptations.

There is a critical period in the life cycle of the desert birds which makes them particularly susceptible to ground predators. This is the nesting period when the birds return to or remain in the same site for a long period. It is during this period that rodents, snakes and other terrestrial enemies have a greater chance of finding their prey than is the case during non-breeding times. This is well substantiated by MACLEAN (1970a), who found that only 18 % of eggs produced by larks produced fledglings. This is half of the mean over five years of 39 % success of the Cape Bulbul eggs (LIVERSIDGE, 1970) which was already considered abnormally low (RICKLEFS, 1969).

In terms of proximal factors the stimulus that attracts a bird to a certain area is little understood; HILDEN regards it as a psychic factor. Such a view is over-simplistic and it is generally agreed there are certain physical parameters that birds select.

The second set of proximal factors are nesting sites, song sites etc. Here we have the specific factor which influences each individual species. MacLean (1976) has shown very well how important the nest site is to desert species. As regards nest sites the main problems are thermo-regulation (Bartholomew, White & Howell, 1976), predation (MacLean, 1970a) and availability (MacLean, 1976). The third proximal factor mentioned is food supply.

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The Evolution of Habitat Specializations in Space and Time

Allen Keast

Avian habitat may be thought of at two levels, from the viewpoint of the individual species, and in terms of faunas and communities. Because birds are so dependent on vegetation habitat specialization is largely towards a specific type or formation. The habitat is a major ecological attribute of the individual species. It provides cover, food and breeding site. During its evolution the species adapts so as to optimize on the opportunities the habitat provides. The major vegetation formations of any continent are characterized by distinct faunas or associations of species—see Hall & Moreau (1970) for Africa.

The present paper investigates the evolution of habitat specializations or "preferences" in avian species.

What is avian habitat?

To consider avian habitat as simply synonymous with a gross vegetation type is an oversimplication. Some "generalist" species range through several vegetation types. The habitat sometimes varies geographically (see later). Where very different vegetation types (e.g. rain forest and woodland) come together there is an abrupt changeover of bird species. But where there is a sequence of gradually changing vegetation types (M. L. Cody, this volume) species limits are vague. Altitudinal zonation is a feature of high mountains and each zone has its own avifauna; Terborgh (1971), however, found variation in the extent that species from one zone penetrated another. Further complications are that some species occupy only part of a vegetation zone, or are restricted to scattered pockets in a seemingly homogeneous habitat (Diamond, 1973). Some are linked to a minor feature within a formation, e.g. hemlocks and pines in the Nearctic parulid, *Dendroica fusca.*

The spatial separation of congeners

Congeners within avifaunas are characteristically separated spatially, i.e. they occupy different geographic areas, habitats, or feed at different vertical levels. Striking examples are provided by the larks and pipits in Africa, honeyeaters and warblers in Australia. Only occasionally are the separations not highly visible. But note here the complex interrelationships of some parulid warbler species (MacArthur, 1958).

How do habitat specializations and separations evolve? The evidence is that they arise mainly at two points in the geographic speciation sequence, when during isolation the daughter populations are subject to differential selection pressures and when the former isolates, now reproductively distinct, come together. Charles Darwin, trying to explain differentiation on islands, suggested that no two were quite identical as physical and biotic environments. This is certainly true of the large segments of continents.

Studies of speciation in Australia (Keast, 1961) show the most important areas of isolation and differentiation to be the northwest, northeast, southeast, and southwest

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"corners" of the continent (see *Platycercus* and *Melithreptus* in Fig. 1). As environments these differ as follows. The north has mean winter temperatures of 21—24 °C, the south 10—13 °C. The north has a summer rainfall; the southeast winter and summer rains, and the southwest only the former (Leeper, 1960). The northwest is covered by tropical woodland, the northeast (which has mountains) by woodland and rain forest, and the southeast by temperate forest and woodland. The southwest, which is isolated by arid terrain, has only a small area of forest and woodland. The first three have rich avifaunas with species replacement, the southwest is depauperate. Thus, new species evolving in the four segments will be subject to different environments, including combinations of competitors, to which they must adapt or perish. The differing ecologies achieved could, however, favour coexistence if as a result of climatic change these new species expand their ranges and meet.

Mayr (1942) and Lack (1944) postulated that when two reproductively isolated daughter populations come together the following may happen: (a) one may prove superior and eliminate the other, (b) they may form a contact zone, each keeping to where it is best adapted, or (c) occupy different habitats or vertical feeding zones. In later years there have been comprehensive documentations of how one animal species may modify the ecology of another (Nilsson, 1963; Diamond, 1973; Des Granges & Grant, 1979). These observations argue that the terminal stage of the speciation process is important in fixing habitat differences.

The evolution of habitat specializations and differences in Australian bird species

The Australian continent, with its simple climatic and vegetation zoning, is an appropriate stage on which to test the above. Here there is a wide range of genera whose species separate out on habitat.

Two examples are given in Fig. 1: *Gerygone*, with the ranges of 5 of the 8 Australian species plotted; and *Pardalotus*, with 6 of the 8. The maps show species in these genera restricted to rain forest, mangroves, sclerophyll (eucalypt) forest, woodland, mallee, and the arid interior. Commonly there is limited range overlap at the habitat edges. The freely hybridizing *Pardalotus striatus* complex (that includes *melanocephalus*), inhabiting dry sclerophyll forest and woodland, extends into the desert along the rivers.

How do these habitat differences arise? A range of intermediate stages in their evolution can be demonstrated, though many of the separations involve different species groups and are presumably old.

Isolation, differentiation, and the production of differently-adapted counterparts

The *Platycercus eximius* and *Melithreptus lunatus* superspecies provide examples of differentiating forms in the four "corners" of the continent (see also Keast, 1961). In the former (where the forms are sufficiently distinct to be called species) all remain isolated except *adscitus* and *eximius* in the east (demonstrating that reproductive distinctness has not been achieved). Many other genera are represented by disjunct forms in the northwest and northeast (e.g. *Psephotus, Poecilodryas, Climacteris*); most also remain isolated. Of those that have bridged the arid Carpentaria barrier *Meliphaga flavescens* apparently meets its eastern counterpart *(M. fusca)* but *Poephila cincta*, and *P. bichenovii*

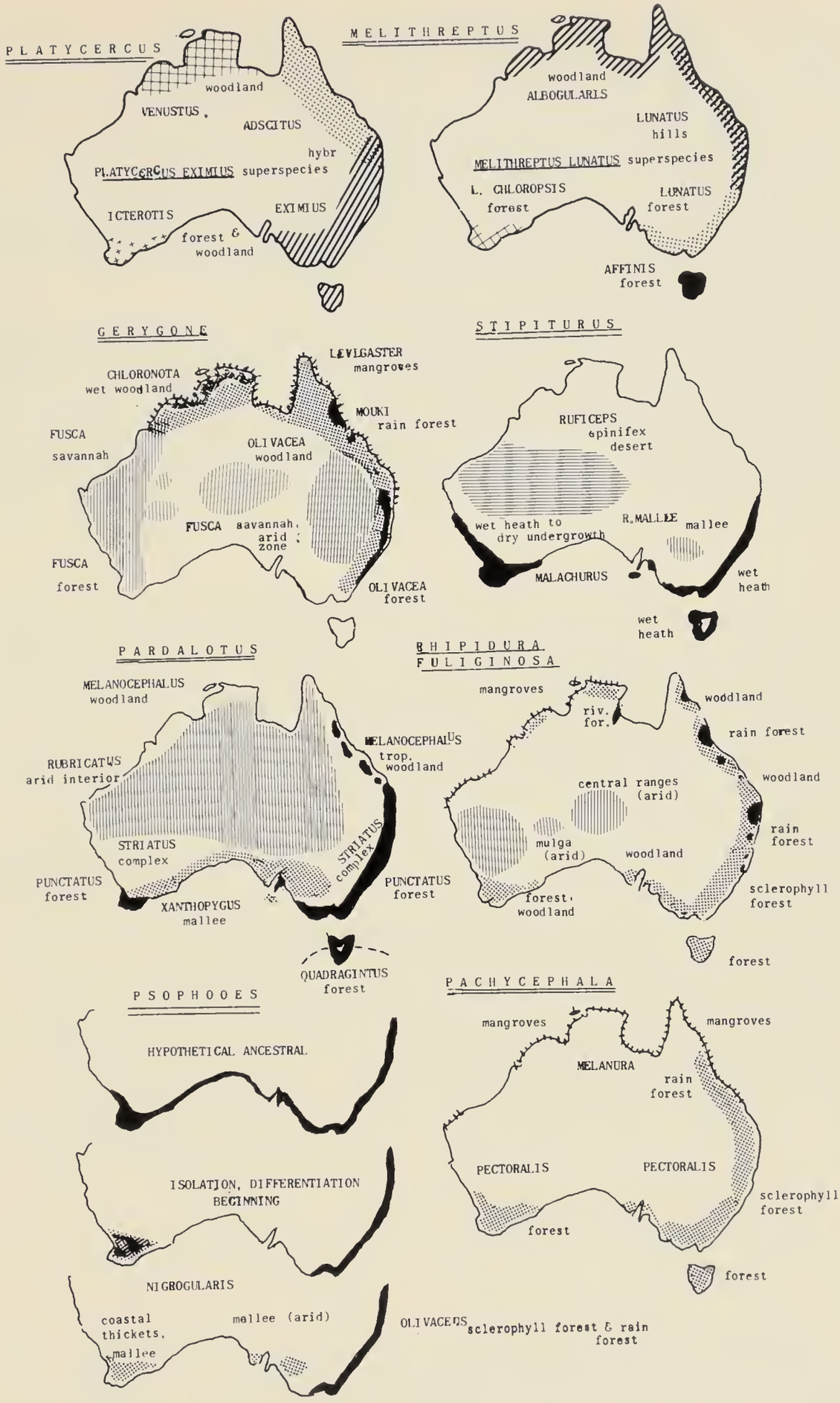

FIGURE 1. Habitat specialization and its development in various genera and species groups of Australian birds (see text).

further west, form hybrid zones. Because the northwestern and northeastern environments are similar it is doubtful if counterparts derived here are differently adapted.

Between the northeast and southeast of the continent there is much species replacement. As would be expected, the northern subtropical woodland and southern eucalypt forest species are somewhat differently adapted. This is shown by the tendency of the latter to become highland dwellers in the north *(Sericornis frontalis, Pardalotus punctatus),* with the southern *Meliphaga lewini* here being replaced in the lowlands by a close relative, *M. notata.* Some northern rain forest species are lowland dwellers in the southern parts of their range.

The isolated southwestern corner of the continent is peculiar in that the area of forest and woodland is small, there are no mountains so the area is vulnerable to climatic deterioration, the summer is dry, and mallee (a dry-country formation) intrudes on the forest. Here eastern "wet country" species may cling to the restricted forest (e.g. *Pardalotus punctatus*—Fig. 1) or occasionally show unexpected adaptability and extend into the dry country, e.g. *Stipiturus malachurus* (Fig. 1), and *Rhipidura fuliginosa* (J. Ford, pers. comm.).

The production of desert and arid-adapted species from coastal ones

Since many Australian interior birds show striking physiological and ecological adaptations (Dawson, 1979; Serventy, 1971) a long history of desert life is indicated. Yet workers (e.g. Schodde, 1976) see many interior species as derived from coastal ones. To produce a desert species, as distinct from a dry-adapted population of a coastal one, isolation has to occur. Presumably desert forms have been "budded off" in different ways (note that the nearest relative of *Meliphaga virescens* is the mangrove *M. fasciogularis*). The southwest, however, would seem to have played an important role. Note the intermediate geographical position and habitat plasticity of the southwest population of *Stipiturus malachurus* relative to the eastern wet-adapted *malachurus* and desert interior *ruficeps* and *r. mallee* (Fig. 1). Mallee, an arid-adapted association of stunted eucalypts with multiple trunk systems and growing on sand, which extends across southern Australia, has about 10 endemic bird species. In the east of the continent the mallee and coastal forest avifaunas are spatially separated and distinct. Some mallee species have apparently been generated via the southwestern pathway; *Psophodes nigrogularis* is an example. It is suggested that the ancestral *Psophodes* originally extended right along the south coast but the southwestern population became isolated by aridity and the formation of the Great Australian Bight. It differentiated and adapted to dry conditions and, thus equipped, was able to expand eastwards with the mallee habitat. Note that various mallee forms occur on the coast in the southwest *(Leipoa ocellata)* and some species have populations in the southwest and eastern mallee *(Glossopsitta porphyrocephala).*

Adaptation from forest to woodland or mangroves, and vice versa

Although good demonstrations of these pathways are limited this is probably because in the east forest and woodland share a common front for hundreds of miles. Whilst some species are shared and forest species penetrate woodlands along the rivers, large segments of the avifaunas are different. In the past there may have been species differ-

entiation to the east and west of the Great Divide when it was a cooler and higher barrier. Many, however, probably stem from the northern woodland belt. Rain forest species are, for the most part, highly distinct from south temperate forest ones. Many of them belong to New Guinea groups and have invaded from there. There are, however, a few cases where southern forest species are represented by rain forest populations in the north (e.g. *Climacteris leucophaea-minor).*

Mangrove species are probably also mostly invaders from the north. *Rhipidura fuliginosa* and *Pachycephala pectoralis-melanura,* however, suggest a pathway whereby mangrove species might be derived from southern forest ones. The former, a small aerial feeding flycatcher, has a largely peripheral range, with many disjunct populations; on the west coast only mangroves apparently supply vegetation of the right type and it is a mangrove species. Though many of the populations are differentiated all are allopatric and conspecificity is assumed. In the thickhead, *Pachycephala,* by contrast, a rather poorly differentiated mangrove form *(melanura)* extends southwards through that habitat to occur side-by-side with an eastern rain forest one (GALBRAITH, 1967; MACDONALD, 1973).

Habitat separation in the presence of a congener

Whether a primary event (achieved ahead of meeting the congener) or a secondary one (partly the result of interaction with it), various cases of allopatric forms separating into different habitat where they meet can be demonstrated. Examples occur in *Melithreptus,* where *M. albogularis* (northern form) inhabits the lowlands and *M. lunatus* (southern) is confined to the hills (Fig. 1); the wrens *Malurus elegans-pulcherrimus-lamberti* (SERVENTY, 1951); *Pachycephala pectoralis-melanura* and, probably, *P. rufogularis-inornata* (KEAST, 1961). In two cases of speciation by double invasion in Tasmania *(Pardalotus quadragintus-punctatus*—Fig. 1—and *Sericornis magnus-frontalis)* and one in the southwest *(Eopsaltria georgiana-australis),* the range of the earlier invader has been compressed by the later one. The regularity with which congeners replace each other in adjacent habitats, and respond to an absence by expanding the habitat and feeding zone, is proof of continuing interactions. Examples of the latter include invasion of the trunk-feeding adaptive zone by meliphagids and *Colluricincla* in Tasmania (which lacks trunk feeders—KEAST, 1970) and the invasion of the southwestern forest by interior species, e.g. *Gerygone fusca* in the absence of *G. olivacea* (Fig. 1), and the meliphagids *Meliphaga virescens* and *Lichmera indistincta.* The southwest has only 13 species of woodland-forest honeyeaters compared to 23 in the southwest.

The avifaunas of the major vegetation formations

In an earlier survey (KEAST, 1961) the writer calculated that 16 % of Australian bird species were confined to, or had their centre of abundance in, rain forest, 16 % sclerophyll forest, 2 % mallee, and 3 % mangroves, whilst 28 % occurred mainly in woodland. The fact that it is possible to come up with such a grouping means that major sections of the avifauna are coevolving and subject to common influences. These "habitat associations" are, however, composites of species of different "ages" (endemic genera to recent colonizing species) and species having different degrees and patterns of dependency on the formation. Wide spectra of ecological types are present but the

associations are not integrated units, rather they are combinations of species with common needs.

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Morphologie und Habitatnutzung europäischer *Acrocephalus*-Arten

Bernd Leisler

Einleitung

Rohrsänger *(Acrocephalus)* sind eine Gattung der Grasmücken (Sylviinae), die sich als Lebensraum die Verlandungszone von Gewässern, besonders der gemäßigten Breiten, erschlossen hat. Hier bilden sie einfache Vogelgemeinschaften, die hauptsächlich die aufragenden Pflanzen der Verlandungsgesellschaften bewohnen. Ihre ökologische Isolierung und ihr Artenreichtum prädestinieren die Rohrsänger für Untersuchungen der Einnischung.

Seit langem ist Ornithologen bekannt, daß sich jede der sechs mitteleuropäischen *Acrocephalus*-Arten [die im folgenden verwendeten Abkürzungen in Klammern, drei einfarbige: *A. arundinaceus* (Aa), *A. scirpaceus* (As), *A. palustris* (Ap), drei gestreifte: *A. melanopogon* (Am), *A. schoenobaenus* (Asch), *A. paludicola* (Apa)] an einer bestimmten Stelle der Verlandungszone in bestimmtem Pflanzenwuchs findet. Durchquert man in einem günstigen Gebiet Europas die Verlandungszone vom Land zum offenen Wasser, so kann man längs des Habitatgradienten „zunehmende Feuchtigkeit" bis zu sechs Arten aufgereiht finden. Insgesamt sind die drei einfarbigen Arten in ihrem Vorkommen stärker abhängig von aufragenden starren Pflanzen als die drei gestreiften, die mehr Unterwuchsbewohner sind (Leisler 1977).

Der Lebensraum

Merkmale von Verlandungszonen sind: 1. eine geringe Vegetationshöhe und geringe vertikale Strukturierung, 2. extreme Bedingungen für Vögel durch die Summierung vieler gleicher vertikaler Halme (Koenig 1952); daher kommen nur wenige Mitbewohner vor, 3. sehr hohe Produktivität (Whittaker 1975) mit geringer jährlicher Fluktuation des Nahrungsangebots, 4. trotz der zeitlichen Abfolge, der Sukzession, hohe Stabilität. Bestimmte Pflanzengesellschaften bestehen über sehr lange Zeiträume.

Aus diesen Merkmalen resultiert für die einzelnen Vogelarten eine hohe Voraussagbarkeit der Ressourcen und der Mitbewohner (möglicher Konkurrenten). Nach den Merkmalen 3 und 4 läßt sich eine geringe Nischenbreite der Arten voraussagen (s. MacArthur & Levins 1967).

Habitataufteilung

Um zu sehen, nach welchen Variablen die Habitate der sechs Arten getrennt sind, wurden an vier Punkten Europas (Hortobágy, Ungarn: Apa, Asch; Neusiedler See, Österreich: Asch, Am, Ap, As, Aa; Bodensee, Südwestdeutschland: Ap, As, Aa; Carmargue, Südfrankreich: Am, As, Aa) in den Revieren der Rohrsänger folgende Merkmale gemessen: Wassertiefe, Vegetationshöhe, Anteil aufragender starrer Halme/qm und horizontale Vegetationsdichte ("half covered board method", MacArthur & MacArthur 1961, Cody & Walter 1976). Vegetationsprofile wurden gezeichnet und deren Gesamtfläche bzw. deren Teilflächen in 0,5 m Höhenintervallen über Boden oder Wasser gewertet. Die Merkmale wurden einer Diskriminanzanalyse unterzogen.

Die Wassertiefe trennt die Arten am schärfsten. Abb. 1 zeigt die dreidimensionale Ordinierung der sechs Arten. Diskriminanzachse I ist Ausdruck eines Gradienten vom Land zum offenen Wasser (sie hat positive Korrelationen mit der Wassertiefe 0,85, der Vegetationshöhe 0,81, der Anzahl aufragender Elemente 0,68 und mit den Teilflächen 8 und 9, d. i. höher als 2 bis 2,5 m). Diskriminanzachse II führt zu einer trockeneren Situation mit vielen aufragenden Elementen. Auch die Diskriminanzachse III trennt gut nach abnehmender Profilfläche und abnehmender Zahl aufragender Elemente. Unabhängig von der floristischen Zusammensetzung ist die von den einzelnen Arten in den verschiedenen Gebieten bewohnte Vegetationsstruktur sehr ähnlich (s. MacArthur et al. 1962).

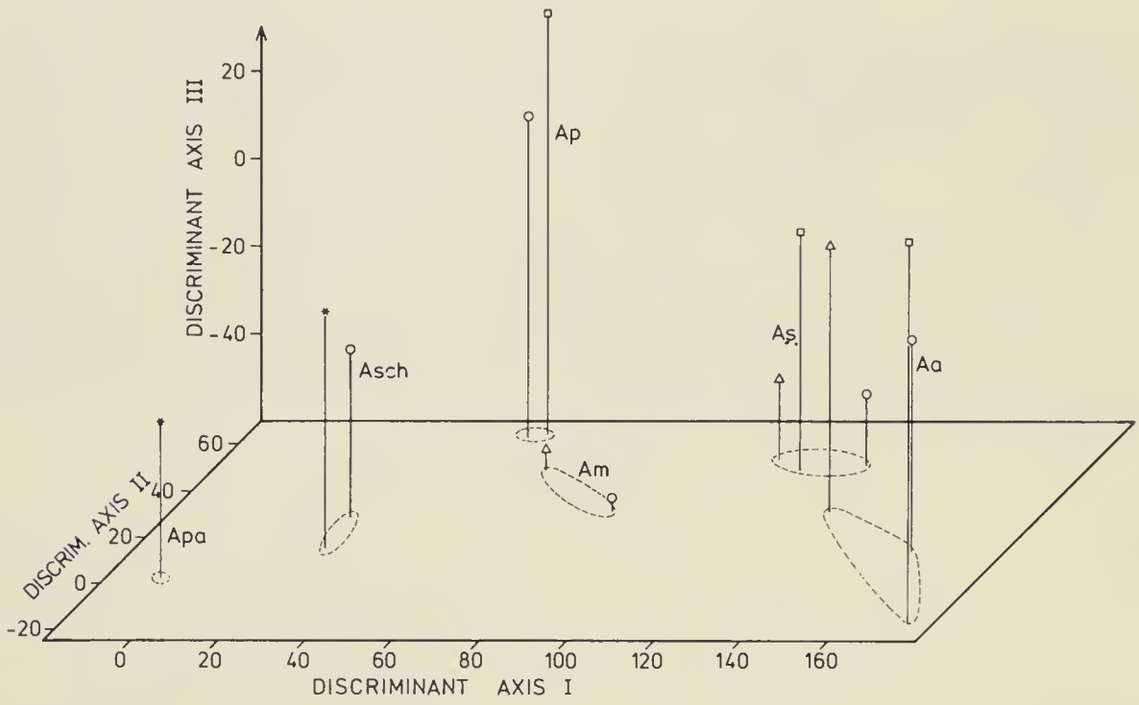

Abb. 1. Ordinierung der Habitate von 6 *Acrocephalus*-Arten nach einer Diskriminanzanalyse von 12 Habitatmerkmalen. Achse I bedeutet zunehmende Wassertiefe, Vegetationshöhe, Anzahl aufragender Elemente und Schwerpunkt der Vegetation in den höheren Schichten. Achse II bedeutet abnehmende Wassertiefe, zunehmende Anzahl von aufragenden Elementen. Achse III bedeutet abnehmende Fläche des Vegetationsprofils, abnehmende Anzahl aufragender Elemente. Abkürzung der Arten im Text. Symbole: ★ Ungarn, O Neusiedler See, □ Bodensee, △ Camargue.

Three-dimensional ordination of the habitats of 6 *Acrocephalus*-species according to the first three discriminant axes. Axis I is a gradient from land to open water (it is correlated to increasing water depth, vegetation height, number of emergent elements and has high profile areas in the upper levels), axis II leads to a drier situation with many emergent elements, axis III represents decreasing profile area and number of emergent elements.

Die sechs Arten sind ökologisch hauptsächlich räumlich — durch unterschiedliche horizontale Habitatselektion — getrennt. Geringe Unterschiede in der Futterselektion und in der Brutphänologie tragen zu weiterer Trennung bei (Leisler, in Vorbereitung). Eine ähnlich präzise Habitataufteilung wurde in ähnlich einfachen Lebensräumen bei *Cisticola*-Arten (Ruwet 1964) und bei grasbewohnenden Emberizinen festgestellt (Cody 1968).

Morphologische Anpassungen

Im folgenden möchte ich auf die Fragen eingehen: 1. was die Gattung befähigt hat, diesen extremen Lebensraum zu besiedeln (also was die Basisanpassungen an den Lebensraum sind) und 2. welche spezialisierenden Anpassungen die einzelnen Arten entwickelt haben. Vergleicht man die Rohrsänger mit ihren ökologischen Vertretern in anderen Kontinenten, zeigt sich, daß die Schlüsselanpassungen für die Besiedlung von Röhrichten das Klettern an Vertikalhalmen und die Nestanbringung an bzw. zwischen Halmen sein dürften (LEISLER 1977).

Um die spezialisierenden Anpassungen herauszufinden, wurden Merkmale einzelner morphologischer Funktionskomplexe der sechs *Acrocephalus*-Arten mittels Hauptkomponentenanalysen (PCA) mit denen zweier ökologisch wie systematisch nahestehender Gattungen *(Sylvia* und *Locustella)* verglichen. Die beiden Gattungen schließen an *Acrocephalus* ökologisch insofern an, als sich *Locustella* den Bereich der feuchten Kraut- und Strauchschicht erschlossen hat, während Grasmücken zusätzlich noch die Baumschicht bewohnen. Die Hauptkomponentenanalyse mehrerer Merkmale eines Funktionskomplexes zeigt, wie ähnlich die morphologische Struktur bei den untersuchten Einheiten ist bzw. inwieweit sie sich differenziert hat. Da verschieden große Arten verglichen werden, wurden alle Meßwerte größentransformiert. Diese Analysen ermöglichen einige Voraussagen über die Rolle der Körperstruktur bei der Habitatnutzung der Gattung bzw. der Arten. Eine Untersuchung von drei Funktionskomplexen brachte folgende Ergebnisse (LEISLER 1977):

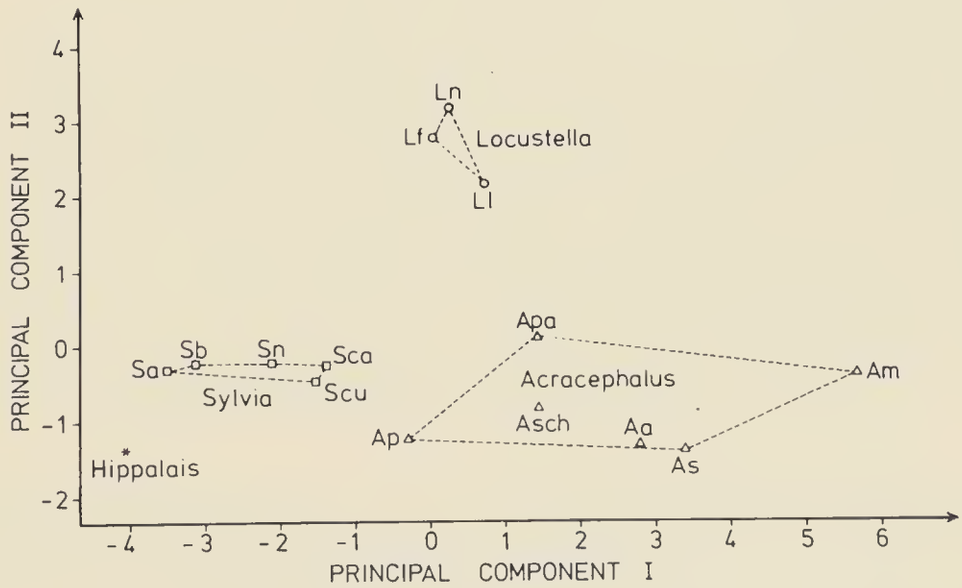

Abb. 2. Hauptkomponentenanalyse von 10 Merkmalen des Funktionskomplexes „Fuß" einiger mitteleuropäischer Sylviinen. Komponente I repräsentiert zunehmende Klammerfußeigenschaften, Komponente II zunehmende Stand/Lauffußeigenschaften.
Abkürzungen und Symbole: *Locustella* = ○, Ln = *L. naevia*, Ll = *L. luscinioides*, Lf = *L. fluviatilis; Sylvia* = □, Sa = *S. atricapilla*, Sb = *S. borin*, Sn = *S. nisoria*, Sco = *S. communis*, Scu = *S. curruca; Acrocephalus* = △, Ap = *A. palustris*, Apa = *A. paludicola*, Asch = *A. schoenobaenus*, Aa = *A. arundinaceus*, As = *A. scirpaceus*, Am = *A. melanopogon*, ★ = *Hippolais icterina*.

Ordination of some Central European sylviid warblers on the first two principal components constructed by analysis of 10 characters of the foot functional complex. Component I represents increasing qualities of a climbing foot, component II increasing qualities of a walking foot.

Hinterer Bewegungsapparat: Wie für Klettervögel ohne Stützschwanz an vertikalen Substraten zu erwarten (Winkler & Bock 1976), haben Rohrsänger lange, stark beugbare Beine. Die einfarbigen Arten und der Mariskensänger sind in diesem Merkmal stärker spezialisiert als Schilf- und Seggenrohrsänger, die beiden Unterwuchsbewohner am landseitigen Ende des Habitatgradienten.

Fuß: Zehn Fußmerkmale (Fußspanne mit und ohne Krallen, Länge der vier Zehen und der vier Krallen) wurden untersucht (Abb. 2). Hauptkomponente (PC) I faßt Merkmale eines Klammerfußes zusammen (Korrelationen mit allen Merkmalen, also großer Fuß mit besonders langer Hinterzehe und Hinterkralle). Komponente II charakterisiert einen Stand-/Lauffuß mit langer Mittel- und Innenzehe und kurzen Krallen. Die Rohrsänger haben sich im Fußbau stark differenziert (s. auch Leisler 1975). Die starken Spezialisierungen im Bau von Fuß und hinterem Bewegungsapparat lassen bedeutende Lokomotionsunterschiede erwarten, die wohl in Anpassung an verschiedene Habitatstrukturen entwickelt wurden.

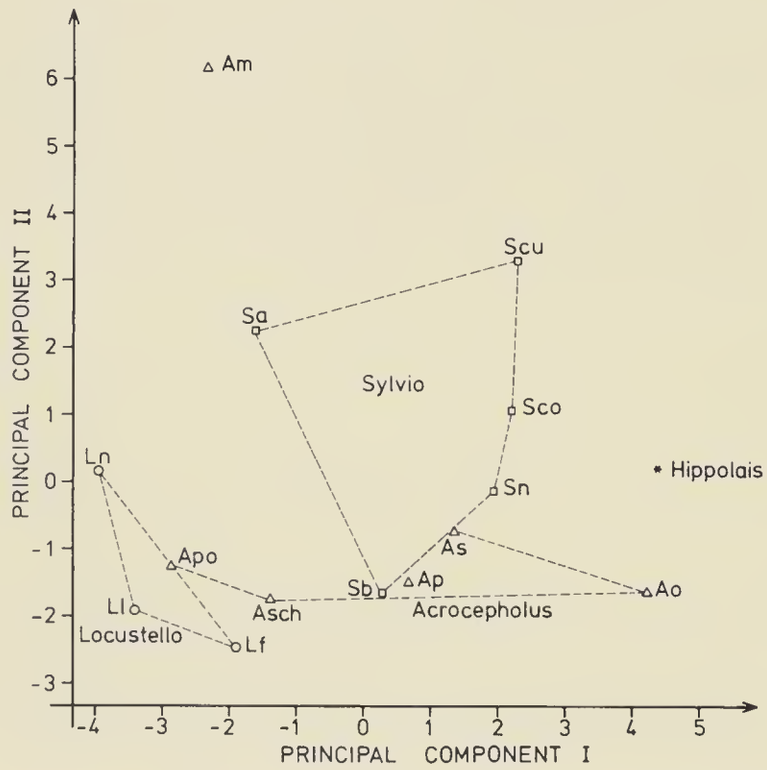

Abb. 3. Hauptkomponentenanalyse von 18 Merkmalen des Funktionskomplexes „Flugapparatur" einiger mitteleuropäischer Sylviinen. Komponente I repräsentiert zunehmende Eigenschaften von Streckenfliegern (Spitzflügeligkeit etc.), Komponente II zunehmende Eigenschaften von Eckenfliegern (Rundflügeligkeit etc.).
Abkürzungen und Symbole wie in Abb. 2.

Ordination of some Central European sylviid warblers on the first two principal components constructed by analysis of 18 characters of the flight apparatus. Component I represents increasing qualities of high performance fliers, component II increasing qualities of thicket fliers.

Nahrungsapparat: Auch die Schnabelunterschiede sind beachtlich, etwa im Vergleich zu *Sylvia*. So haben die landseitigen Vertreter zum Abklauben geeignete Schnäbel ausgebildet, die wassernah lebenden Vertreter (Teich- und Drosselrohrsänger) zum Fang sehr beweglicher Beute geeignete Schnäbel.

Flugapparatur: Es wurden 18 Merkmale des Großgefieders untersucht (s. Leisler 1980). Hauptkomponente I faßt Merkmale von Streckenfliegern zusammen (Lang-, Spitzflügeligkeit, gerade abgeschnittener Schwanz), Hauptkomponente II Merkmale von Dickicht- d. h. „Ecken"-fliegern mit hoher Manövrierfähigkeit (Rundflügeligkeit, breiter Armflügel, Schlitzbildung der Handschwinge). Die untersuchten Einheiten gruppieren sich folgend (Abb. 3): Schlechte Flieger finden sich links unten, das sind die Schwirle *(Locustella)* und der Seggenrohrsänger (Apa), die als extreme Unterwuchsbewohner nur wenig fliegen. Die Rohrsänger sind in Komponente I weit auseinandergezogen. Es fällt auf, daß die Arten (abgesehen vom Mariskensänger, Am) in derselben Reihe erscheinen wie auf der Diskriminanzachse I (s. Abb. 1). Da alle Arten Transsaharazieher sind (Moreau 1972), bedeutet das, daß sie vom Seggen- (Apa) zum Drosselrohrsänger (Aa) in zunehmendem Maße den Flügel bei der Habitatausnutzung gebrauchen, und zwar um so mehr, je höher die Vegetation wird und je mehr sich das Pflanzenvolumen von der untersten Schicht nach oben verlagert. Weiter fällt auf, daß sich die Rohrsänger, obwohl Bewohner von vergitterten Lebensräumen, im Hinblick auf Manövrierfähigkeit (Komponente II) nicht differenziert haben. Alle liegen etwa auf einer Linie. Die isolierte Stellung des Mariskensängers (Am) erklärt sich daraus, daß er im Gegensatz zu allen anderen untersuchten Arten als Teilzieher bzw. Standvogel (Leisler 1973) keinen Zugflügel entwickeln mußte. Als Dickichtvogel konnte er einen extrem manövrierfähigen Flügel bauen. Sehr unterschiedliche Flugfähigkeiten haben die Grasmücken *(Sylvia)* entwickelt.

Körpergröße: Unterschiede der Körpergröße habe ich nach Gewicht und Körpermaß (einem komplexen Rumpfskelettmaß) untersucht (Größenangaben finden sich in Leisler 1975, 1977; für *Sylvia* wurden Gewichtsdaten aus Mazzucco 1974 verwendet). Um einen Meßwert für den Größenunterschied der Arten zu erhalten, habe ich innerhalb einer Gattung die Arten nach Gewicht bzw. Körpermaß geordnet und dann den Wert der größeren Art durch den der nächst kleineren dividiert. Die Quotienten wurden für die Gattungen gemittelt. Als Mittel für die Gattungen ergeben sich bei *Sylvia* (5 Arten) 1,22 bzw. 1,24; bei *Locustella* (3 Arten) 1,19 bzw. 1,17 und bei *Acrocephalus* (ohne Aa 5 Arten) 1,02 bzw. 1,09. Hohe Mittel haben Grasmücken *(Sylvia)* und Schwirle *(Locustella)*, das heißt, sie sind verschieden groß. Dagegen haben sich Rohrsänger bis auf den großen Sprung zum Drosselrohrsänger (der nicht berücksichtigt wurde) größenmäßig wenig differenziert.

Diskussion und Schlußbetrachtung

Zusammenfassend läßt sich sagen: Bei ihrer Radiation in verschiedene Ausschnitte der Verlandungszone mußten sich die Rohrsänger an verschiedene Vegetationsstrukturen sehr fein anpassen. So erfolgten starke Spezialisierungen im Bau der Hinterextremität und des Fußes und im Schnabelbau, weniger im Flügelbau. Nach den Befunden von Ricklefs & Cox (1977) über die Beziehung zwischen morphologischer Ähnlichkeit und ökologischer Überlappung läßt sich voraussagen, daß bei den Rohrsängerarten Unterschiede sowohl in der Methode wie auch im Ort der Nahrungssuche bestehen dürften. Offensichtlich bedingt durch die dichte Struktur der bewohnten Vegetation, konnten sich Rohrsänger in der Körpergröße nur wenig differenzieren.

Abschließend seien einige Spekulationen über Evolution und Alter dieser Vogelgemeinschaft vorgebracht. Nach paläobotanischen Daten existierten die charakteristischen Pflanzengattungen der Schilfröhrichte *Typha, Scirpus* und *Phragmites* bereits zu Ende der Kreidezeit und Anfang der Tertiär (Lamotte 1952, Gothan & Weyland 1954, Hultén 1962). Röhrichte sind also sehr alte Lebensräume. Auf den verschiedenen Kontinenten wurden sie von ganz verschiedenen Sperlingsvogelgruppen besiedelt (nur Arten berücksichtigt, die diesen Lebensraum sowohl zur Brut als auch zur Nahrungssuche nutzen): in Europa und Afrika von Sylviinen, besonders in Asien zusätzlich von Timalien; in Nordamerika von Icteriden, Troglodytiden und Emberizinen (v. Udvardy 1958), in Südamerika von Furnariiden und Tyranniden (Keast 1972) — also stets von wenigen, sehr erfolgreichen, vielseitigen Gruppen. Das legt nahe, daß die Besiedlungen nicht sehr alt sind und erst gelangen, als aus diesen Gruppen sich Formen mit entsprechenden Präadaptationen für eine Besiedlung entwickelt hatten. v. Udvardy (1958) hat aus der „unvollständigen" Anpassung der sumpfbewohnenden amerikanischen Sperlingsvögel an den Lebensraum auf eine junge Abstammung von typisch baumbewohnenden Gattungen und Familien geschlossen. Er verwies auch auf die Existenz freier ökologischer Planstellen für bestimmte Lebensformen in den Röhrichten auf verschiedenen Kontinenten.

Herrn Dr. H. Winkler (Wien) danke ich für die Berechnung der multivariaten Statistik.

Summary

Morphology and habitat utilization in *Acrocephalus* in Europe.

In Europe 6 *Acrocephalus* species (3 plainbacked: *A. arundinaceus, A. scirpaceus, A. palustris* and 3 streaked: *A. schoenobaenus, A. paludicola, A. melanopogon)* inhabit marshes, especially the emergent vegetation of water and littoral plant communities. Characteristics of such habitats are 1. low vegetation height and vertical stratification, 2. uniform vegetation and thus a structurally simple habitat with only few coinhabiting bird species, 3. high productivity and low annual fluctuations of food supply, 4. despite vegetational succession, high stability of the habitat. A high predictability of resources as well as of coinhabitants result from these characters. Being very habitat-specific the 6 species are separated ecologically mainly by differences in horizontal habitat selection. A comparison with reed bed inhabiting ecological equivalents shows that the basic adaptations for invading such a habitat might be nest suspension and climbing vertical stems. Dense vegetation structure may have prevented the reed warblers from radiating into different body sizes. An analysis of some morphological functional complexes (foot, hind limb, feeding apparatus, flight apparatus) with the aid of multivariate statistics shows to what degree the species have stayed similar or differentiated. Corresponding to the vegetation structures occupied, the 6 *Acrocephalus* warblers have developed different specializing adaptations in all morphological complexes analysed except the wing.

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SYMPOSIUM ON RESOURCE UTILIZATION, COMPETITION AND AVIAN COMMUNITY STRUCTURE

7. VI. 1978

CONVENERS: J. WIENS AND J. NEWTON

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Spatial and Resource-Use Patterns in Wintering Shorebirds: The Sanderling in Central Coastal California

F. A. Pitelka, J. P. Myers and P. G. Connors

Wintering shorebirds of a variety of species can coexist in coastal habitats in relatively stable numbers for a period of months – five to six months in central coastal California. These communities, uncomplicated by the overlay of breeding activity, raise interesting basic questions regarding between-species competition and the structuring of shorebird assemblages. But such studies are difficult for a number of reasons, one of them being that we need to know a lot more than we do today, first, about the feeding and spacing behavior of individual species, at the population level; and second, about the food resources they exploit. Only with such information can we achieve the basic perspective needed to assess and interpret between-species effects.

This caution was forced upon us in our studies of shorebird feeding and spacing behavior on Bodega Bay 75 km north of San Francisco. We begin with several facts of basic natural history.

In a mixed local fauna of winter-season shorebirds – 18 species in our case – foraging occurs either territorially or non-territorially, the latter usually meaning in flocks. This is true of many species including the Sanderling *Calidris alba.* Some species are consistently non-territorial (e.g., Marbled Godwit *Limosa fedoa,* Dunlin *Calidris alpina,* Short-billed Dowitcher *Limnodromus griseus);* but others, even if strongly territorial, are not consistently so, and instead show variable spacing patterns of territoriality and flocking. Further, the extent of territoriality varies across habitats. Thus, the Sanderling can be territorial on outer beaches, it is less so on protected lagoon sand flats, and only rarely so in the rocky intertidal. Moreover, among the shorebirds in our local fauna, the overall proportion of individuals that are territorial differs from one species to another. The magnitude of this intra- and inter-specific variation emphasizes the importance of spacing and feeding patterns in relation to two aspects of habitat: first, the set of interspersed intertidal habitats available around Bodega Bay; and second, the proportional areas of these habitats and the varying periodicities of their tidal exposure. This is the stage for our research.

With Wagnerian ambition, we chose three species showing mixed spacing behavior – the Black-bellied Plover *Charadrius squatarola,* Willet *Catoptrophorus semipalmatus,* and Sanderling – and our objective was to compare their feeding and spacing behavior with relation to habitat and prey. But we soon realized that our time-energy budgets were strained: variable foraging behavior, with at times both flocking and territoriality of one species in one habitat, requires a knowledge of its food base, not only densities of the chief prey species, but especially their variation in space and time. The scale of this effort, with no existing information to fall back on, forced us to confine ourselves to one species. We chose the Sanderling. We monitor its numbers and local movements over the area as a whole, but up to now we have studied its behavior in relation to food supply mainly on open beaches. There the study of prey is relatively easy because the important items are

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few and easy to sample. They are mainly crustaceans, sand crabs *(Emerita)* and isopods *(Excirolana)*.

Our local population of Sanderlings has been censused over two winter seasons, and in the period 1 October to 1 April it averages about 500 birds. In the past three seasons, we have color-banded over 250 individuals, and of these 120 were present in 1977–78. Returns for adults run 70%, those for birds banded in their first year 50%. Like other wintering shorebirds banded and recaptured in following years, the Sanderling is remarkably area-faithful. Checks to the north and south of Bodega Bay have yielded less than 2% of banded individuals.

Territoriality in Sanderlings occurs most strongly on outer beaches, and at times the entire 3.7 km length of one of our study beaches may be defended territorially by a linear sequence of birds, averaging roughly 50 m per bird. Wintering Sanderlings defend sites with classically territorial behavior, including aggressive displays and vocalizations, frequent chases, and border encounters. Territories mapped repeatedly through time show that boundaries can be remarkably fixed, with most individuals occupying sites on successive tides, as demonstrated by repeated sightings of color-banded birds. Some occupy a given territory over months, and a few do so even in consecutive years. But others switch intermittently to flock, and finally there are those, again color-banded, which forage only in flocks. Territorial individuals can be of either sex, and either adult or first-year.

Up to a quarter of the local birds are territorial during one or another part of the winter, with territoriality most common during fall and early winter. The incidence of territoriality changes with prey abundance. Birds are less likely to defend if food density at a site is very high, or if it is too low. Thus there appear to be upper and lower threshold densities of prey in outer beaches which set constraints on when and where birds will defend. From a sequence of intensive samplings, mainly in 1977–78, we find that territorial behavior is strongest when combined and adjusted densities of the two main prey items (sand crabs and isopods) are between 400 and 1600/m^2.

The aspect of our work we want to develop in some detail in what follows concerns the timing of habitat use by the two alternative behavioral modes – territorial and non-territorial. As we have described, the Sanderling population at Bodega Bay depends on resources in two habitats. We have quantified the time trend of the between-habitat movement, and we have related variation in this pattern to the behavioral modes of the Sanderlings and to seasonal variation in prey density. As an example, we first summarize data from early November 1976 gathered over a 12-day period which spans a typical range of tidal patterns. Study plots consist of two separate beaches (1 km length of each) and a lagoon sand flat (plot 1 km x 200 m). Censusing is done hourly and simultaneously on the three study areas by three observers through the daylight hours and on four days.

Sanderling numbers change progressively throughout the day on each transect. Numbers fluctuate each day from high densities, sometimes over 100 per km, down to zero. This fluctuation corresponds closely to change in tide level: Sanderlings move to outer sand beaches and forage there during high tide, but as the tide recedes they move to the sandy flats of the lagoon. Thus the tidal regime introduces a cyclic rhythm into their foraging location. By moving from location to location, Sanderlings expand the portion of the tidal cycle during which they can forage.

During this 12-day period, Sanderlings defended relatively stable territories on one of the censused beaches. Daily counts of territories in a 1-km strip ranged from 25 to 31. During most censuses, non-territorial birds were also present on the beach, but they differed from the territorial birds in their dependence on beach resources. Calculating the percent of daylight hours during which the tide is below 3 feet, we find that on days when low tides occupy more of the daylight foraging hours, all Sanderlings spend less time on outer beaches. Territorial birds, however, consistently spend more time on the beaches than the competing, roaming hoodlum flocks. The territorial birds arrive sooner, and stay longer in the daylight portion of each lunar day, perhaps merely to reclaim and hold their territories, or perhaps also to benefit directly from the actual advantages of the territory. These could be increased foraging efficiency, or reduced exposure to predators, or some other benefits.

These results suggest a simple graphical model comparing feeding efficiencies of territorial and non-territorial birds on sandy beach in relation to their feeding efficiency on lagoon flats; i.e., how do their respective efficiencies vary with tide height on the two sites? Because of the intertidal zonation of Sanderlings' major prey items on the beach, they are most available at tide heights between +3 and +5 feet. At lower tide levels the prey are less accessible because the sand dries to a hard matrix and becomes more difficult to penetrate. Thus foraging efficiency decreases on the beach as the tide goes out. On the lagoon flats, in contrast, our sampling shows that prey density – and we infer feeding efficiency – rises within the foraging positions favored by Sanderlings to a maximum at low tide levels. We postulate that feeding efficiency is the critical factor determining the choice of foraging area: Sanderlings move to one habitat or the other depending upon where they will forage most successfully. We further assume that territorial birds are more successful on the beach at the same tide level than are non-territorial birds. Combining these relationships we obtain a set of curves that predict territorial birds should stay longer on the beach, a pattern observed in our data.

It follows that if food conditions change in one habitat relative to the other (beach versus lagoon flat), we should observe a change in the birds' time budgets in these habitats. Such a change comes strongly each spring when the last larval stage of the sand crab *Emerita* settles out in high densities on the beaches. This happens rather suddenly. There is an overall five-fold increase in density of sand crab larvae in late March. Foraging efficiency of birds does not necessarily change by the same factor, but it surely increases significantly. The result is a strong difference between November and April in time spent on the beach. After the increase in beach prey density, birds depart from the beach at a significantly lower tide level than they did in November. We consider these results to be consistent with our view that habitat time budgets are determined by relative foraging efficiencies in the different habitats.

In summary, first, Sanderlings move between habitats on a regular tidal schedule to increase their potential foraging time. Second, their habitat time budgets adjust to changes in food conditions which presumably effect changes in foraging efficiency. Third, different behavioral classes of Sanderlings exhibit differences in their habitat time budgets. We regard these to reflect differences between the two classes in foraging efficiency within one habitat (beach). And fourth, and more generally, the alternative strategies of spacing and foraging – that is, territorial versus flocking behavior – represent a basic pattern in social

organization not only of wintering Sanderlings but a significant number of other non-breeding shorebirds yet to be studied. As is well known, diversity of habitat in an area promotes diversity of species present there, but local diversity in intertidal habitats is increased by differing tidal schedules and differing cross-tidal distributions of prey abundances. The result is that opportunities for food exploitation shift regularly in time and space. For Sanderlings, the resources available on outer beaches are surely a critical dimension in competition, not only intraspecifically, but interspecifically as well. Along the California coast generally, local densities are lower where the mosaic of outer beaches and lagoon flats is lacking. Were the Bodega system, for example, to lose its sandy beaches (we are, after all, situated directly on the San Andreas Fault!), local Sanderlings would not only suffer the loss of their high-tide foraging area, but they would also be forced to forage entirely where the species diversity of shorebirds is highest locally. Thus the demands of inter- and intra-specific competition, which encourage the Sanderling's spatial and temporal exploitation of the habitat mosaic, ultimately underlie their behavioral plasticity and heterogeneous spacing pattern.

As the foregoing makes clear, much of our effort is devoted to questions of foraging efficiency and especially to the population ecology of several important prey species. These are studies in progress on which we expect to report in detail elsewhere. At this time, our main point is the fact of behavioral variability in use of space and exploitation of resources in wintering shorebirds. Attention to this variability clearly becomes a necessary part of any study of competition in systems of wintering shorebirds. There is a front of interest in this group that has been expanding rapidly in the last five years, and much exciting work is underway or is being published from Pacific as well as Atlantic coasts. Easy to observe and offering considerable variety in behavior, both intra- and interspecifically, they can yield much of basic interest to current thinking about adaptive strategies and competition.

Acknowledgements

Our research has been supported by National Science Foundation grants. Additional support has been provided by the University of California Sea Grant Program. We appreciate assistance and facilities made available by Professor Cadet Hand, Director of the Bodega Marine Laboratory. Field assistance was provided by Carolyn Connors, David Shuford, James R. Weinberg, Brian S. Yandell, and J. Stephen Yaninek.

Intra- and Interspecific Competition for Space in Estuarine Bird Species in a One-Prey Situation

Leo Zwarts

Introduction: habitat segregation in a field study

Many studies have shown that there is habitat segregation in coexisting animal species. This is often explained by the competitive exclusion principle, which implies that species have evolved so as to avoid competition. Less common are field studies concerning the question to what degree habitat selection as we see it today is determined by ongoing interspecific competition.

Intertidal mudflats, where in general many migratory bird species feed at high densities and often in continually changing mixed-species assemblages, offer an opportunity to investigate change in dispersion, habitat shift, or decrease in numbers as a consequence of the presence of other species. Since there are many complicating factors, it remains difficult to prove competition in a field study.

A unique opportunity to study intra- and interspecific competition occurred at an intertidal mudflat (North-Ventjager, Holland) where the ragworm *Nereis diversicolor* was the only available prey. In spite of this, the shorebird diversity was as high as on other European intertidal flats where ten or more prey species comprise the diet.

Size selection of *Nereis* by waders

Size selection was investigated in one part of the study area during nine low water periods in April and May 1968. No data are available on average weight and density of *Nereis* during the two observation months, but two months afterwards, in July, the density of *Nereis* appeared to be very high (3320 ± 800 worms per m^2, n = 30) and the average weight very low (5–10 mg ash free dry weight).

The capture rate of *Nereis* was measured for eleven bird species and appeared to be lowest in the Dunlin *Calidris alpina:* 2 *Nereis*/min, and highest in the Black-tailed Godwit *Limosa limosa:* 12.7 *Nereis*/min. In all species the range of the capture rate was rather narrow (coefficient of variation 32% on average), except in the Oystercatcher *Haematopus ostralegus* where prey capture was variable: birds pecking and probing obtained respectively 18.4 and 3.8 *Nereis*/min. Birds which caught worms from a greater depth obtained on average fewer worms per unit of time ($r = -.43$, $p = .14$, $n = 12$), but the average weight increased (Fig. 1), which was to be expected since large *Nereis* occur at greater depth than smaller ones (Muus, 1967). The average prey weight for each species was estimated by assuming that the daily existence energy equals 3.5 times basal metabolism (King, 1974), that the digestive efficiency of worms is 85%, and that the feeding success and activity at low water during day and night is the same. This "guestimated" gross food intake was divided by the number of *Nereis* taken (average capture rate multiplied by the known feeding time at low water), to obtain the probable weight of an average *Nereis* per bird species. As expected, the greater the pecking-depth the larger the prey, but as shown in

Ysselmeerpolders Development Authority, Smedinghuis, Lelystad, Holland.

Fig. 1, most species took *Nereis* of about the same size. Though the data cannot be used to calculate the overlap in vertical feeding range and in prey size, it may be assumed that overlap between most species was large.

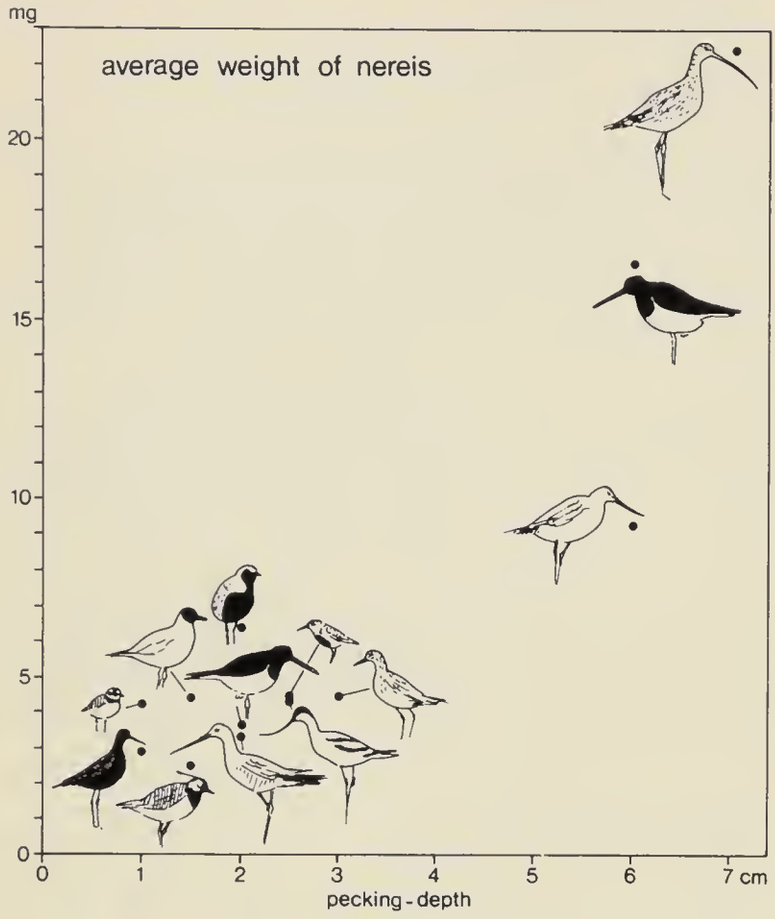

FIGURE 1. The average prey-weight (ash-free dry) as a function of the average depth from which the prey is obtained. All data are from the same spot and the same time. The regression X = 4.16 Y + 8.44 is significant, r = .90.

Time and space

There was a nearly complete overlap in the feeding time during the tidal cycle, because all birds fed during the seven hours that the *Nereis*-area was uncovered. There was also a broad overlap in the seasonal occurrence: 15 of 19 wading birds and gulls which occurred regularly on the Ventjager reached their peak number between 25 July and 15 September.

There was some segregation between the species regarding the *Nereis*-area exploited (Fig. 2). Avocet *Recurvirostra avosetta* do not feed on mud where the clay content is below 10% because, as suggested by TJALLINGII (1972), an Avocet catching *Nereis* by sweeping the bill through the substrate, cannot do so if the soil resistance is too high.

On the Ventjager Avocet, Spotted Redshank *Tringa erythropus* and Black-tailed Godwit were only observed feeding on the soft substrate (area B and D), whilst on the other hand Bar-tailed Godwit *Limosa lapponica,* Kentish Plover *Charadrius alexandrinus* and Oystercatcher only caught *Nereis* on the sandflats (area A, C and NE part of D).

Intraspecific competition

It is to be expected that each species would select those parts of the area where it is profitable to feed. If at an increasing density the tendency to concentrate on optimal feeding areas is counteracted by the presence of other birds there, the consequence can be a change in the dispersion pattern or a decrease in the proportion of birds feeding. Both

changes were observed in Teal *Anas crecca* on the South-Ventjager (ZWARTS, 1976) and also in several waders.

The dispersion pattern has been analysed for 51 low water counts of the Ventjager in relation to density in nine bird species (ZWARTS, 1974). The relative numbers on D were found to decrease at higher total numbers in six species, in two there was no change and in one species an increase (Fig. 2). A was only an important feeding area if many birds were present: in eight species the proportion visiting A went up at higher total densities and in only one species was there a slight relative decrease. Taking all species together, 10% of all birds fed on A at low densities and 30% if many birds were present.

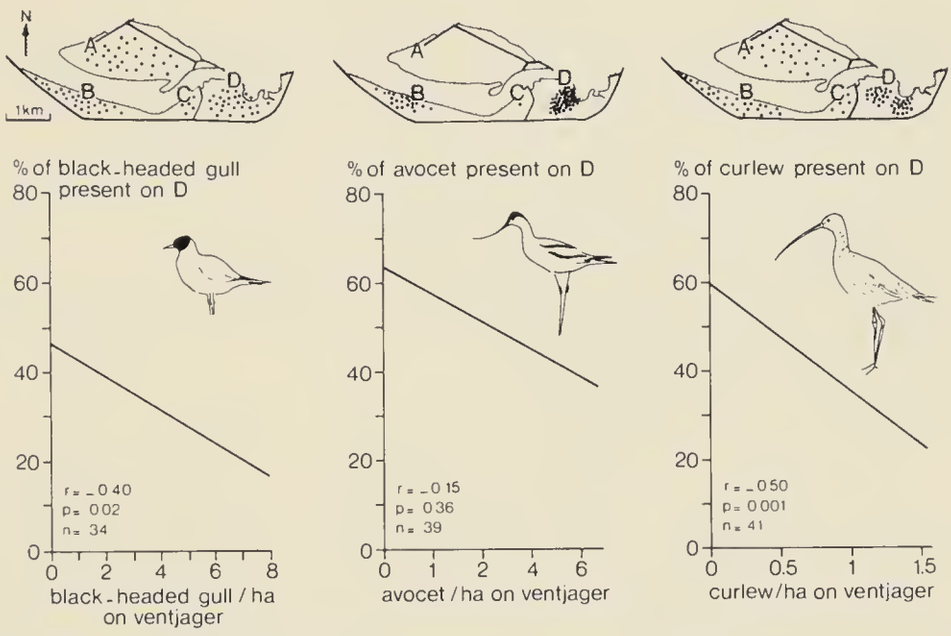

FIGURE 2. Average distribution of Black-headed Gull, Avocet, and Curlew on the North-Ventjager at low water (51 counts in 4 years, each dot is 1%). The graphs show that the proportion of the birds feeding on D is dependent on the total number present. The density on D does not increase above an average density of .9 Curlew and 5 Black-headed Gull/ha on the Ventjager (910 ha).

No data are available for feeding success on A, so it is not possible to relate the feeding profitability on A and D, apparently marginal and optimal feeding areas (but see GOSS-CUSTARD, 1977). It is also possible that distance between roost and feeding area has to be taken into account to explain this density-related dispersion (HAMILTON & WATT, 1970). The flight distance for A and D amounted to respectively 3.5 and 2 km. In nearly all bird species there appeared to be a positive correlation between the total number present and the average flight distance.

If, as on the Ventjager, the dispersion seems density-related, it is of interest to determine the maximal feeding density in the areas where the numbers were buffered, especially because all species took the same prey. The maximal density of the bird species feeding on *Nereis* appeared to be dependent on the weight of the avian predator, but plovers fed at much lower densities (Fig. 3).

The maximal densities are taken from 51 low water counts on A, B, C and D (surfaces 20–143 ha). On counting sites of smaller size (1 and 0.1 ha) the observed maximal feeding densities were about 5 times as high as on A, B, C or D, but the same trend was

found. For the Curlew *Numenius arquata* data are available (Fig. 4) which show that at a density above 10 Curlew/ha – the maximum on the Ventjager – the intake of *Nereis* goes down. If the prey is the crab *Carcinus maenas,* the penalty for feeding in high densities is less direct. It is not yet clear what is the relative importance of both mechanisms suggested by Goss-Custard (1970): resource depression and interference.

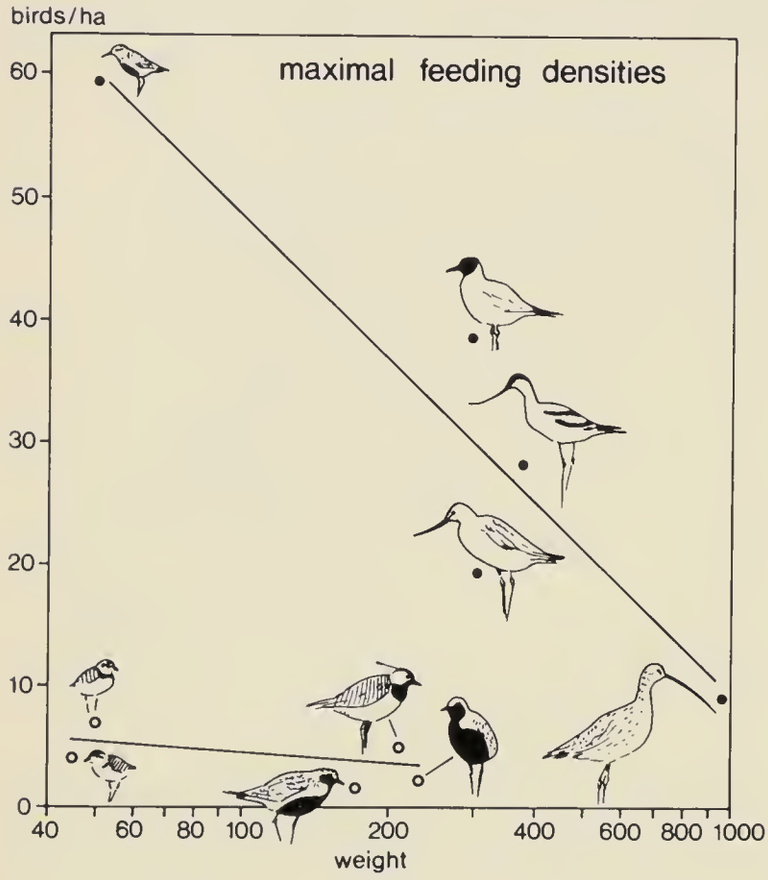

Figure 3. Maximal densities of ten bird species preying upon *Nereis* in A, B, C or D (see Fig. 2), plotted against log weight. The regression for the plovers is not significant (r = –.47). The other slope differs significantly from zero (r = –.94).

It can be supposed that the feeding density is in some way a functional adaptation to the density of the available, suitable prey (see Schoener 1970). For a Curlew (900 g.) taking larger worms than the Dunlin (50 g.), see Fig. 1, the density of suitable prey-items was much lower since large worms were rare. So perhaps a Curlew taking *Nereis* has to search a larger area than a Dunlin to satisfy its energy requirements, which can be achieved by an increase of the search-path, and/or by broadening the search-field. A widened search-field in larger birds is likely because the height of the eye above the substrate increases: if the densities in Fig. 3 are replotted against eye-height the figure does not change much. If there is such an increase in search-area in larger birds, it is likely that each bird claims a larger personal field, which results in the lower feeding density.

The same kind of reasoning can be applied to understand the relatively low feeding densities of the five plovers. Plovers are sit-and-wait predators which use a space-consuming feeding strategy because the *Nereis* they detect by eye form only a small fraction of the total number of *Nereis* present in the mud.

If the maximal feeding densities, converted to log feeding area/bird, is related to log weight, the slope for the five plovers is 0.58 and for the five other bird species 1.34,

which is very close to the exponential relation calculated by SCHOENER for territory size and weight of avian predators.

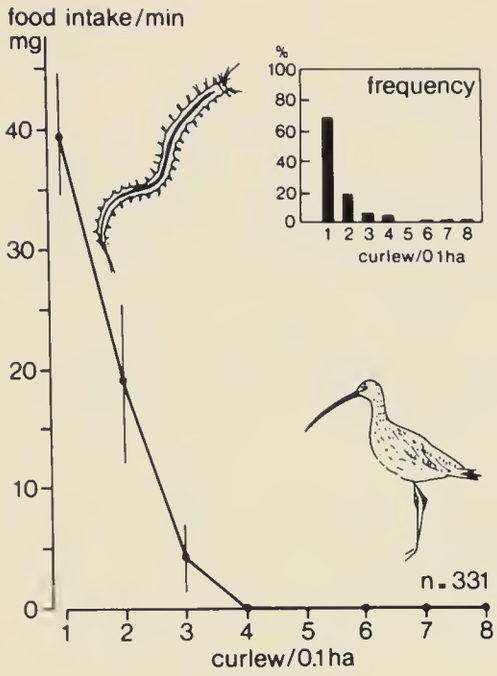

FIGURE 4. The food intake (mean ± standard error) of Curlew taking only *Nereis* during the observation periods (each 1–10 minutes) as a function of the number of Curlews feeding in counting sites of 1000 m^2 (Frisian coast, summer 1977).

Interspecific competition

If it is true that within a species an increasing feeding density causes a lower food intake because of resource depression and/or interference with each other's search path, it is likely that the presence of birds of another species will have the same effect on the feeding success. This has not yet been studied but some data on the dispersion pattern suggest that birds are avoiding parts of the feeding area which are occupied by other bird species. Detailed maps of the low water dispersion of Black-headed Gull, Avocet, and Curlew on D on 11 days (given by ZWARTS, 1974) showed that Avocet and Black-headed Gull did not mix: both species fed in flocks, each day occupying different but always mutually exclusive areas. The Curlew fed scattered on a fixed part of D.

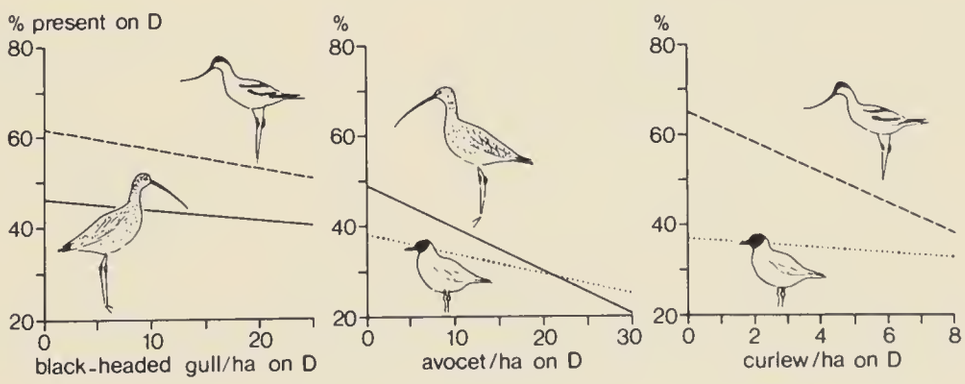

FIGURE 5. The proportion of the birds on the Ventjager feeding on D as a function of the density of another species on D, holding constant in a multiple regression analysis the effect of low water level and total number of their own species. In the simple regressions the interspecific effects are more pronounced; the mutual effects of Curlew and Avocet are significant ($p = .01$).

Since the data in Fig. 2 suggest that D was probably a preferred feeding area for all bird species, it is to be expected that if there was a tendency to avoid areas occupied by another species, the proportion of the birds which made the choice to feed there was dependent on the number of individuals of another species present. Fig. 5 shows that this was indeed the case.

Acknowledgements

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On some Relationships between Energy and Diversity Models of Ecosystems

Steven Cousins

Introduction

Energy modellers and diversity modellers adopt radically different approaches to the study of community ecology. Whole system energy models such as that recommended for use in the International Biological Program (Petrusewicz & Macfadyen, 1970) depend on partitioning the ecosystem into a few discrete compartments, trophic levels, and measuring the biomass at, and energy flows between, compartments. This method ignores species identity within each level and the complexity of species interactions between levels. However, it would also be difficult if not impossible to provide a meaningful diversity index of a trophic level since each level will include species from many classes from protozoa to vertebrata.

Species diversity modellers stress the importance of complexity of interaction between species as a fundamental variable of interest yet their unit, the taxon, includes species which are, according to trophic level descriptions, as unrelated as herbivores, carnivores and detritovores.

Both schools of thought use their models to approach the question of the stability of ecosystems, the diversity-stability relationship being one field of endeavour, and stability as a function of the number of trophic levels (Pimm & Lawton, 1977) another.

Energy models

The opportunity to suggest that there is a much closer relationship between the analysis of energy flow and the study of species diversity comes from a reassessment of how we model energy flow. Earlier this century the study of trophic interactions, later to become ecosystem energetics, was centred on examining the abundance of organisms of different size classes. These were represented as a pyramid of number or Elton's pyramid in which the ecosystem was populated by a few large and a progressively larger number of smaller organisms. Hardy (1924) described how the herring's food web interactions change with changing size (age) of the fish. In 1927 Elton wrote: "Size has a remarkably great influence on the organisation of animal communities. We have already seen how animals form food chains in which the species become progressively larger in size, or in the case of parasites, smaller in size. A little consideration will show that size is the main reason underlying the existence of these food chains and that it explains many phenomena connected with the food cycle (web)".

A lower limit on the size of food taken may be considered (Schoener, 1971) to arise from the costs in time and energy of the search, capture and chemical reassortment of the prey. An upper limit can be defined by the inability of the would-be predator to pursue and subdue the prey item – again neatly summarized by Elton as "Spiders do not catch elephants in their webs nor do water scorpions prey on geese".

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In short, scattered packets of energy are harvested by larger organisms at an energy cost of collection and processing. The balance of that energy transaction has been collected into a larger packet – the ingesting organism itself – which is then available for ingestion by still larger organisms.

This process of energy concentration also occurs in the green plant, but it is not determined by ingestion. This is the fundamental point of departure from LINDEMANS (1942) trophic level model. Energy can change its packet size or its concentration, i.e. change its state in trophic space in ways other than ingestion although this is the principal method in the interactions between animals. In plants this is achieved by translocation and chemical transformation creating a variety of states from low energy density foods such as leaf drip up to high energy density seeds and reproductive units shown as A_m to A_n in Figure 1. Detritus may also be conceived of as a variety of energy densities or packets which are in a general state of disintegration by the process of weathering, and dismembering by detritovores D_n to D_m. Thus detritus too can change state without being ingested. Animal size classes, H_3 greater than H_2 etc, are shown in the central row of Figure 1. A minimum of connecting flows are shown in Figure 1: double arrowheads indicate a feeding flow, single arrowheads a non-feeding flow; no respiratory flows are shown. The abundance of organisms in each H state gives ELTON's pyramid, although biomass in energy flux can replace abundance as a measure.

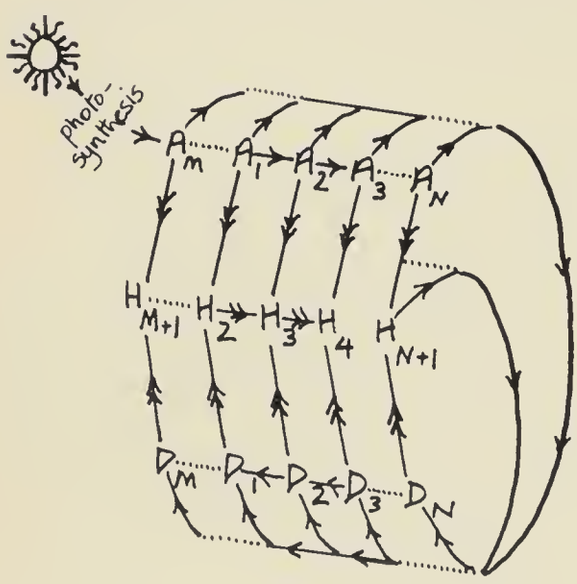

FIGURE 1. A trophic continuum. For explanation, see the text.

The variety of energy states in the green plant have different entropies and cannot be summed to give a reference point for the interactions of heterotrophs. This is, however, the whole basis of the LINDEMAN model. Similarly the variety of detritus states cannot be summed in order to scale heterotroph interactions. Heterotrophs may, however, be studied using body size classes as a descriptor of trophic state. For clarification consider the following example.

A slice of bread eaten by humans sustains human action; if the bread is divided into eight pieces and scattered over an ecosystem, say a field, then the likelihood of the bread becoming human food is diminished and the chance of it being ingested by birds and small mammals increases; if it is split into a thousand pieces and distributed, the likelihood of

ingestion by birds and mammals decreases and ingestion by collembola, beetles and worms is greater; if it is pulped in water and sprayed thinly over the system only bacteria and fungi are the likely feeders. At any point in this process the sum of energy or the material inputs to the system is constant. Yet the entropy, the quantity of disorder that the food represents, is different in each case.

Elsewhere I have developed the argument (COUSINS, in press) that a change in the size of energy packets represents a change in entropy and that ELTON's model of the trophic pyramid therefore derives from the second law of thermodynamics as well as the first. In contrast LINDEMAN's model ignores energy states other than the change from food substrate to respiratory products and as such ignores significant second law descriptions of ecosystems.

Diversity

The taxonomic group is the fundamental class studied by diversity modellers. Taxonomic groups are made up of members which generally have similar size. THOMPSON (1916) discussed the importance of size relative to taxonomic classes. THOMPSON's law of form states that if an organism changes size it must also change shape, with large changes in size requiring major changes in the structure of the organism, e.g. there are limits to the size of insects because of tracheal respiration and the possession of an exo- rather than an endoskeleton.

Taxonomic groups are limited in the size range of their member species and therefore limited in their position in trophic space. If we consider the group represented by all breeding bird species in the British Isles then variation in species size is just over three orders of magnitude, from the Goldcrest (5.5 g) to the Mute Swan (11 kg). The distribution of breeding bird species density as a measure of species richness is shown for each order of magnitude in Figures 2–4. Figure 5 shows the overall species density with four 50 x 50 km sample broken down into the species density of 8 size classes.

The maps were produced from those in SHARROCK (1976) by registering the presence of each species in 10 by 10 km areas covering the whole of the British Isles. Grid squares which contained more than 5% open water were excluded, and coastal species density values were obtained using contiguous sample areas along the coast, each sample having the same area as the inland sites. Species density values were interpolated by the SYMAP program using five class intervals between the maximum and minimum species density values in each map. There are just four observations that I wish to make from the figures.

(1) There is a change in the species density of each size class on a north-south axis. Larger numbers of smaller species are found in the south while large species are more numerous in the north. The distribution of the small species is more significant because much of the size differences observed in the larger (greater than 465 g) birds can be attributed to the coastal species. Intermediately sized species show maximum abundance south of the maximum size class peak. The overall species density (Figure 5) does not show any decrease in species richness with northerly latitude, yet the change in species size distribution suggests that the species diversity is differently distributed within the trophic pyramid. Where diversity is distributed within the trophic pyramid may have implications for any diversity-stability relationship.

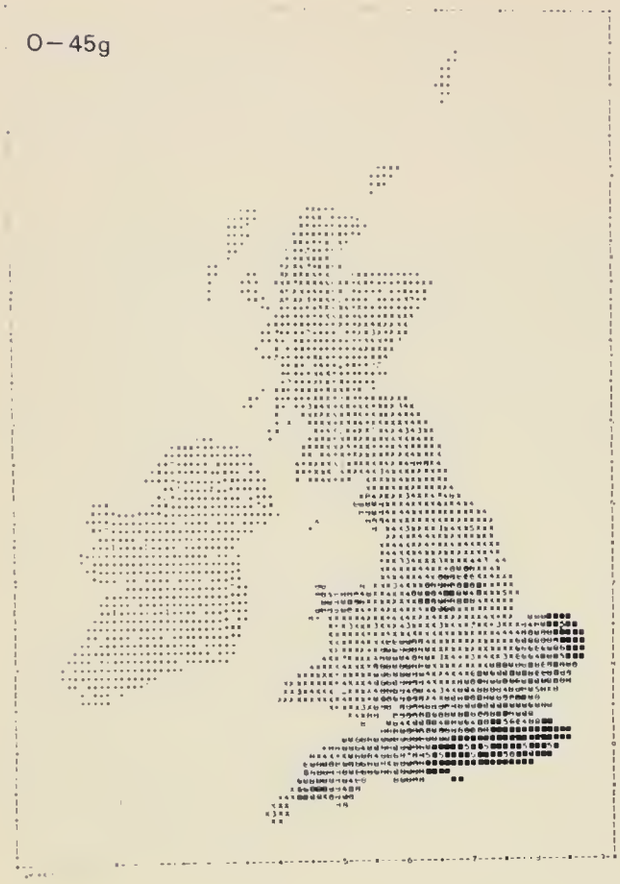

FIGURE 2. Breeding bird species densities for species weighing up to 45 g.

FIGURE 3. Breeding bird species density for species weighing 45–465 g.

FIGURE 4. Breeding bird species density for species weighing more than 465 g.

FIGURE 5. Breeding bird species density for all species, with detailed species size distributions for four 10 x 10 km squares.

(2) The effect of inclusion of a new habitat in the sampling frame is shown by the high species density values of the coastal sites. Much species density work uses a square grid which is only partially filled at coastal sites unlike the present study. The effects of coastal bird diversity is particularly evident in Ireland. This raises the general point that if species richness is generated by a change in habitat and as such represents the discontinuity of subsystems, then species richness may be a measure of disfunction or the heterogeneity of the environment, and there may be no inherent reason for species richness to generate stability.

(3) Why should aquatic birds be so much larger than their land counterparts and what effect does this have on the trophic structure?

(4) Why should there be a gap in species abundance in the 45–105 g class? This gap is also evident in Eltonian pyramids of woodland birds.

Conclusion

Taxonomic groups occupy limited positions in trophic space which may be further delineated by considering particular size classes of the taxon. This is a much closer energy-diversity relationship than was apparent from trophic level concepts. A case has been made that the plant and detritus respectively cannot be used to scale trophic space and therefore that the Lindeman trophic level model does not hold. The species diversity of different size classes has implications for diversity-stability theory but with the constraint that species richness may be a measure of disfunction within an environment.

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Resource Exploitation Patterns and the Structure of a Forest Bird Community

Richard T. Holmes

Introduction

This report is concerned with how food resources are exploited by bird species breeding in a northern hardwoods forest in the northeastern United States. The similarities and differences in foraging patterns among 22 syntopic species, with special emphasis on sexual differences, are examined with the use of multivariate statistical techniques. We have shown in a previous paper (Holmes et al., 1978) that these methods can help to define objecctively the guild structure of a bird community and can identify similar species that may be potential competitors. The factors influencing the observed patterns of resource exploitation and therefore the structure of the bird community are discussed.

Study area and methods

The study was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, USA. The forest consists of an uneven aged, well stocked stand of northern hardwoods, with the canopy height averaging about 25–30 m. The dominant trees are American Beech *(Fagus grandifolia)*, Sugar Maple *(Acer saccharum)*, and Yellow Birch *(Betula lutea)*. Detailed descriptions of the Hubbard Brook forest, its climate and vegetation, and bird communities, can be obtained from Likens & Bormann (1972) and Holmes & Sturges (1975).

Foraging behaviors of bird species breeding in the Hubbard Brook forest were quantified during June and July in 1974, 1975, and 1976. Each time a bird was seen performing a foraging maneuver, the following information was recorded: its species and whenever possible its sex, the time of day, type of foraging maneuver (hover, glean, hawk, probe-drill), the substrate (leaf, twig, bark, ground, etc.) and plant species to which it was directed, the height, and if in a tree, whether it was in the region proximal to the main axis of the tree bole or distal, along the outer halves of branches. The various combinations of these categories resulted in 27 'foraging characters' (Table 1). The rationale for including these particular categories is discussed by Holmes et al. (1978).

Even though many individuals on the study area were individually color-banded, it was not always possible to distinguish sexes, particularly for the ground foraging species such as thrushes. For those species for which sample sizes exceeded at least 50 foraging maneuvers for males and for females, the sexes were separated and treated as separate 'species' in the analysis. For others, the data for the sexes are combined and represent species-typical foraging patterns. A total of 7732 foraging maneuvers and their associated data were used in this analysis. Sample sizes per 'species' ranged from 58 to 687, averaging 221.4.

Multivariate statistical analyses were performed on the data matrix consisting of 35 rows (22 taxonomic species, 13 with males and females considered separately) by 27 columns

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(the foraging characters). The first 24 columns were log-transformed to reduce skewness. The last three did not require transformation. All 27 columns were standardized to bring the means to zero and the variances to 1.0, with the result that each measurement was expressed in standard deviation units from its column mean.

TABLE 1: The rotated factor pattern showing the most heavily weighted factors, either positive or negative, for each of the 27 characters.

	Factors						
	I	II	III	IV	V	VI	
Eigen values	8.57	6.83	2.46	1.51	1.11	1.06	
Factor contribution to community variance (%)	31.74	25.30	9.11	5.58	4.12	3.93	
Cumulative %	31.74	57.04	66.15	71.73	75.85	79.78	ROW SS [1]
1 Hover at Leaf		0.953					0.944
2 Glean at Leaf		0.753					0.816
3 Hover at Branch				0.747			0.778
4 Glean at Branch				0.469			0.662
5 Probe at Branch		–0.904					0.933
6 Hover at Twig			0.556				0.412
7 Glean at Twig			0.469				0.765
8 Hawk		0.750					0.679
9 Glean from Ground	–0.916						0.851
10 Probe into Ground	–0.921						0.857
11 Hover on Trunk				0.810			0.779
12 Glean on Trunk		–0.709					0.780
13 Probe into Trunk		–0.914					0.948
14 Probe into Fallen Dead Wood	–0.895						0.828
15 Proximal						–0.747	0.900
16 Distal		0.877					0.954
17 *Fagus grandifolia*					–0.785		0.726
18 *Acer saccharum*			–0.716				0.757
19 *Betula lutea*	0.871						0.816
20 *Fraxinus americana*					0.701		0.806
21 Other *Acer*	–0.634						0.675
22 *Viburnum alnifolium*	–0.956						0.942
23 Conifer *(Picea, Abies)*			0.760				0.682
24 Herbs and Ferns	–0.947						0.924
25 Foraging Height ($\bar{x}$)	0.948						0.952
26 Foraging Height (1 standard deviation)	0.740						0.834
27 Body weight ($\bar{x}$)		–0.598					0.546

[1] Represents the fraction of the variance of each character explained in 6-space (HOLMES, BONNEY & PACALA, manuscript).

The 35 x 27 'character' matrix (R-technique, SNEATH & SOKAL, 1973) was used for the factor analysis. The matrix of correlations between all of the 27 characters was obtained and the eigen roots and vectors of this matrix calculated. Eigen roots greater than 1.0 were used to calculate a Varimax rotated factor pattern (COOLEY & LOHNES, 1971). Elabor-

ations on this procedure are given by Aspey & Blankenship (1977) and by Holmes et al. (1978).

The transposed (27 x 35) 'species' data matrix (Q-technique, Sneath & Sokal, 1973) was used to calculate the Euclidean distances between all combinations of the 35 'species' in the hyperspace defined by the 27 foraging characters. This distance matrix was subjected to a hierarchical cluster analysis for purposes of illustrating species relationships. The raw data matrix is available from the author upon request.

Results

When the 35 bird 'species' are projected into the hyperspace defined by 27 axes (the foraging characters) and then clustered, they segregate into a number of relatively distinct groupings (Fig. 1). Those groups separated by distances greater than the average Euclidean distance between all combinations of 'species' in the community (7.16 units, in this case) are considered as separate guilds (Holmes et al., 1978), since they represent groups of species that exploit food resources in similar ways.

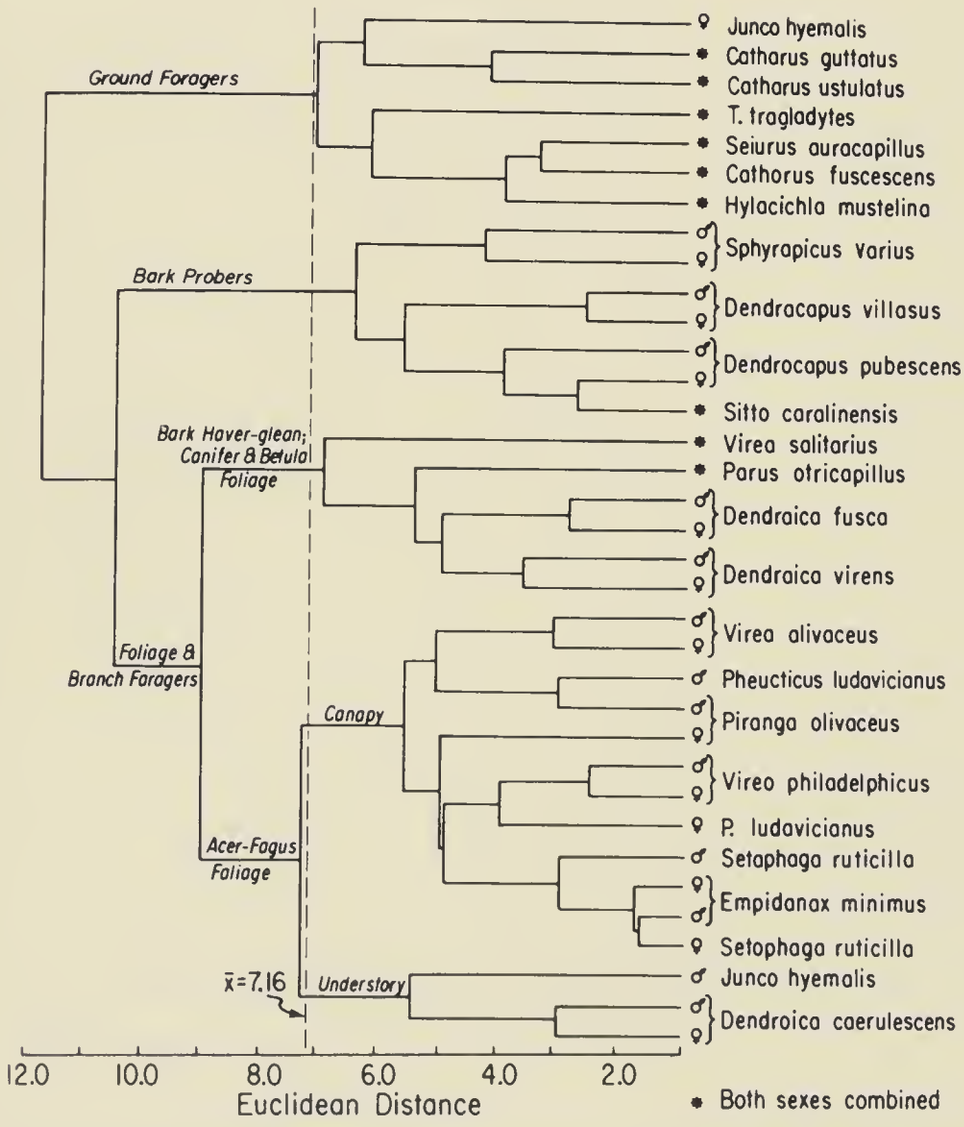

Figure 1: Community dendrogram of Euclidean distance between bird species in the Hubbard Brook forest, indicating differences and similarities in foraging behavior. Dashed line represents the x̄ Euclidean distance between all combinations of species and sexes in the community.

The resulting dendrogram provides a graphical picture of the foraging structure of the bird community and reflects the patterns of food resource partitioning occurring among the 'species'. In most cases, males and females of the same biological species are more similar to one another in their foraging behavior than to any other species (Fig. 1). The most extreme exception is *Junco hyemalis*, in which the females are shown to be more similar to thrushes and other ground foragers while the males resemble *Dendroica caerulescens*, a low understory foliage forager. Other intraspecific differences occur in *Piranga olivaceus* and *Pheucticus ludovicianus*, in which the males are more similar to *Vireo olivaceus* and the females to *V. philadelphicus*. This can be attributed at least in part to height differences; male *Piranga* and *Pheucticus* forage at heights similar to *V. olivaceus* and these are lower than those used by their females and by *V. philadelphicus*. Relatively minor differences occur among the sexes in *Dendrocopus pubescens*, *Setophaga ruticilla*, and *Empidonax minimus*.

To determine objectively the relative importance of the foraging characters responsible for segregating the bird community, a rotated factor analysis was used. This technique weights the variables by their relative contributions to the total community variance and reduces a large number of often correlated variables into a smaller number of identifiable factors that can be used to define the similarities and differences among the 'species' (COOLEY & LOHNES, 1971). This technique is most helpful here at the level of guild separation, and the major findings are labelled on the basal part of the community dendrogram (Fig. 1).

In this analysis, the first two factors account for 66% of the total community variance (Table 1) and the characters contained on them can be considered to be the most important segregators of guilds. Factor I is height-related and separated the ground foragers (the 4 species of thrush, 1 parulid warbler, 1 wren, and the female *Junco hyemalis*) from all other species in the community (Fig. 1). Factor II contains heavy negative loadings for foraging, primarily probing, on bark of tree trunks and positive ones for foraging methods and substrates in the outer regions of the trees, thus separating the bark probing birds (3 species of woodpeckers and 1 nuthatch) from those species foraging among the branches, twigs, and foliage. The correlation of bird size with bark probing (Table 1) is related to the heavier body weights of the woodpeckers.

Factors III and IV, which when combined account for 13.69% of the variance, contain characters which begin to distinguish between the foliage and branch foragers. One group *(Parus atricapillus, Vireo solitarius, Dendroica fusca* and *D. virens)* differ from other species by more frequent hovering and gleaning for prey on twigs, by foraging in conifers and by not foraging in *Acer saccharum*. *Vireo solitarius* is further segregated from this group by its more frequent hovering and gleaning from branches and by hovering for prey on tree trunks (Factor IV, Table 1 and original data matrix).

Factor V contains heavy positive loadings for foraging in *Fraxinus americanus*, a tall canopy emergent, and negative values for *Fagus grandifolia*, which implies that those bird species using one of these tree species as a feeding site rarely use the other. In this case, use of tree species differentiates the foliage foragers into those using the understory (male and female *D. caerulescens* and male *J. hyemalis*) where *Fraxinus* foliage is essentially absent and *Fagus* very abundant, from those species using the forest canopy (Fig. 1). Factor VI, accounting for less than 4% of the variance, cannot be interpreted biologically.

Discussion

The patterns of resource exploitation exhibited by members of the Hubbard Brook bird community (Fig. 1) demonstrate that there are important differences among the species and in some cases between the sexes within a species. Questions then arise concerning what determines these patterns. Have the differences evolved as a means of reducing the effects of competition, as competition theory and many studies imply (e.g. MacArthur, 1958; Cody, 1974; Schoener, 1974)? Or, as suggested recently by Wiens (1977) are they related to other causal factors such as preadaptations for exploiting different resources or habitat characteristics, the effects of predation, physical disturbances, vagaries of climate, etc. In this discussion, I shall consider two factors affecting bird community patterns in north temperate forests; (1) the importance of habitat structure coupled with resource availability, and (2) competitive processes.

Habitat structure and bird community organization

The results of the multivariate analysis demonstrate that certain habitat characteristics, namely vegetation height, structure, and species composition, are important factors affecting the resource exploitation patterns of Hubbard Brook birds. The physical stature of the forest is clearly the most important factor (Table 1) which helps to explain the findings of MacArthur & MacArthur (1961) and others of a relationship between bird species diversity and foliage diversity patterns (Holmes et al., 1978). Besides providing a height gradient of foliage, however, the physical structure also produces several foraging regions – the forest floor, the trunks and large branches of trees, the outer branches and foliage, and an understory layer. Each of these is exploited by relatively distinct groups of bird species (= guilds), with little overlap of species among the regions.

Partitioning on a finer level is achieved by the birds' differential use of plant species, foraging substrates, and foraging maneuvers. These parameters are probably intercorrelated in a complex manner (Holmes et al., 1978). Thus, different plant species often provide different arrays, combinations and abundances of substrates, each with its own characteristic insect fauna (Schultz, 1978). In addition, the branch and leaf arrangements of different plant species may provide either constraints or opportunities for foraging birds (Pearson, 1975). For instance, leaves on long petioles that are situated away from the supporting branches or twigs may make it difficult for a bird to glean an insect, but instead would favor a kind of maneuver in which the bird flies and hovers at the leaf surface. Likewise, the density of branches may determine the frequency and success of birds' hawking insects from the air.

The results of this study therefore indicate that the kinds, distributions and physical arrangements of foraging substrates and probably the abundance and availabilities of their insect faunas, both of which may vary with particular species of plant, are important parameters influencing the ways in which birds exploit and partition their food resources. These foraging opportunities afforded by characteristics of the habitat, in effect, structure the bird community into a number of adaptive types or guilds. What forces, however, drive this apparent specialization and what determines the structure of each guild or the number of species that can exploit these foraging opportunities?

Competition and bird community structure

Competition has long been invoked as an explanation for differences in resource exploitation patterns among sympatric species. WIENS (1977) has recently questioned the assumptions underlying the application of competition theory to studies of bird community patterns, especially those occurring at temperate latitudes, and has called for more specific information documenting the importance of competition in shaping temperate bird communities. Two examples from Hubbard Brook are briefly summarized below, which although not dealing specifically with food resource specializations, do illustrate the role of competition in affecting temperate bird community patterns.

The first line of evidence that competition can be important in affecting community patterns is based on the occurrence of interspecific aggression among ecologically similar species. The most overt example at Hubbard Brook concerns the two species that are most similar in terms of food acquisition (see Fig. 1) – a flycatcher *(Empidonax minimus,* family Tyrannidae) and a warbler *(Setophaga ruticilla,* family Parulidae). These two species overlap significantly in body size and bill morphology, as well as in foraging behavior, and are interspecifically aggressive during the breeding season. Coexistence is mediated by slightly different habitat preferences and by differences in life history characteristics (SHERRY, 1975, and MS). *S. ruticilla* is a broad-niched, behaviorally plastic, socially subordinate, habitat generalist compared to the flycatcher, and its distribution pattern within the Hubbard Brook forest is influenced significantly by the abundance and aggressiveness of *E. minimus* (SHERRY, 1975; PROCTER & HOLMES, unpublished data). The occurrence of this aggression and the distributional shifts argue strongly for the occurrence of on-going competitive interactions.

The second line of evidence concerns the relative importance of interspecific competition in breeding versus winter bird communities. FRETWELL (1972), WIENS (1974, 1977) and others have suggested that population limitation of north-temperate breeding bird species may often occur during the winter season, so that breeding communities are "unsaturated". BENNETT (1978) recently completed a study of the niche characteristics of *Setophaga ruticilla* in several parts of its breeding range, including Hubbard Brook, and in several winter sites, where it coexists with different numbers and constellations of potential competitors. She found patterns among niche breadths, niche overlaps and densities indicating that competition has been important to *S. ruticilla* in both its breeding and wintering areas. She concludes that the effect of competition depends on the birds' energetic demands in relation to the abundance and availability of food resources and on the degree of competitive pressure, both conditions that vary among sites within a season and between different phases of the annual cycle. Thus, population limitation and the relative importance of competition may not occur in either winter or summer, but by processes occurring in both seasons.

Obviously, the factors that limit bird populations and that produce the observed patterns of bird community structures are complex. From our studies at Hubbard Brook, however, I suggest that the structure of the breeding habitat and the food resources it provides are important in providing opportunities for bird foraging specialization, while competitive interactions are or have been a primary factor favoring specific adaptations of bird species to those habitat characteristics. A more detailed understanding of how habitat structure and resource abundance influence bird foraging patterns, particularly through

the use of comparative approaches or manipulative experiments, seems necessary to the further unravelling of these relationships.

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Bird Community Structure in Cold Shrub Deserts: Competition or Chaos?

John A. Wiens and John T. Rotenberry

Introduction

Avian community ecology is concerned with two basic questions: (1) are there consistent patterns of species combinations, guild organization, diversity, community biomass, etc. that characterize species assemblages? and (2) what mechanisms act to produce the patterns, or to thwart their development? The theory that has developed is generally framed in terms of interspecific competition as the mechanism driving community organization: competitive processes among ecologically similar species produce optimal patterns of divergences in resource utilization, placing limits on the numbers and types of species that may coexist (see Schoener, 1974; Cody, 1974; and the papers in Cody & Diamond, 1975). In fact, the occurrence of competition is at times inferred from patterns of community attributes, such as diversity gradients. This view of natural systems has become so entrenched that it is often applied dogmatically, with little consideration of other alternative explanations of the presumed patterns. Recently, however, the ubiquity of this interpretation of community structure has come into question (Caswell, 1976; Wiens, 1977; Connell, 1978).

It is in this context of conceptual uncertainty that we wish to summarize some of the findings of our recent studies in semi-arid shrubsteppe environments of western North America. We emphasize the degree of patterning in breeding avifaunas at regional and local scales and briefly explore some elements of resource partitioning; we can only offer tentative suggestions regarding the mechanisms determining what we observe.

Community patterns: a regional versus a local view

The importante of the geographic scale on which community structure is viewed has generally not been realized (but see Cody, *in* Cody & Diamond, 1975). It is possible that patterns that are apparent at, say, a regional level may not be obvious when communities are viewed continentally or locally. From our studies in shrubsteppe habitats we may ask first whether the avifauna of this habitat in the Pacific Northwest differs from that of surrounding habitat types; that is, whether there are regional patterns. Using roadside censuses conducted in June 1974 as part of the North American Cooperative Breeding Bird Survey (Robbins & Van Velzen, 1967), we analyzed the overall similarities among the counts for 60 separate locations in Washington, Oregon, and Idaho (Rotenberry & Wiens, 1978). If we combine censuses exhibiting more than 50% avifaunal similarity, three major avifaunal regions are apparent: a region in the Ponderosa pine forests of central Oregon; another containing counts in valley to montane deciduous and coniferous forests of western Oregon, western and northern Washington, and northern Idaho; and a third including counts conducted in shrubsteppe habitats of eastern Oregon, southeastern Washington, and southern Idaho. The avifaunal association characterizing the shrubsteppe

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differs in several attributes from those of other regions (Table 1). Species diversity is significantly less there, as are both of its components, species richness and species evenness (an inverse measure of the degree of dominance by a small set of species). The summarizations also suggest that overall densities are greater in the shrubsteppe, although the patterns are not statistically significant.

TABLE 1: Average community attributes of avifaunistically-defined regions and sub-regions in Oregon, Washington, and Idaho.

Region or sub-region [a])	attributes			
	number of individuals [b])	species diversity [c])	species richness [d])	species evenness [e])
High desert plateau (5)	518	3.22	50	0.82
Coniferous/Deciduous forest (25)	606	3.28	52	0.84
Shrubsteppe (29)	706	2.74	41	0.75
Lower Columbia Basin (3)	457	1.76	21	0.57
Transition (2)	547	1.98	24	0.63
Low elevation (11)	868	2.76	41	0.75
High elevation (8)	607	3.23	49	0.83

[a]) Defined by avifaunal similarity; sample size in parentheses, see text.
[b]) Total number recorded per 40-km census route.
[c]) Diversity = $H' = -\sum_{i=1}^{s} p_i \ln p_i$; p_i = relative proportion of the ith species, s = total number of species in the sample.
[d]) Richness = s = total number of species in the sample.
[e]) Evenness = H'/lns.

These regions were initially defined by avifaunal similarities without respect to vegetation, but they coincide closely with the distributions of the respective vegetation formations. The avifaunal patterns are also associated with variations in the climatic regimes of the Pacific Northwest. ROTENBERRY (1978a) defined a multifactorial climatic gradient derived from 15 weather variables through this region; species diversity decreased significantly along the gradient from mild-moist-stable climates to severe-arid-unstable climates, and the diversity changes resulted primarily from variations in the evenness rather than the species richness component.

The breeding bird assemblages of shrubsteppe habitats are thus quantitatively distinct from those of other nearby environments. This is a regional, "between-habitat" community definition, and we may ask whether further patterns exist within the shrubsteppe region. Applying a 67% similarity value to group together censuses from the roadside counts within the shrubsteppe region defines four sub-regions (again defined by avifaunal rather than habitat similarities). The variations in total numbers of individuals are again non-significant, but a collection of "high elevation" (900–1500 m) censuses evidenced greater species diversities than the other sub-regions (Table 1). The relatively lower diversity of the low-elevation sub-region was a function of decreased evenness; that of the lower Columbia Basin and transition areas was associated with decreased species richness.

In addition to these regional and sub-regional patterns in total community attributes, an examination of species' distributions among the census locations reveals that a specific assemblage of bird species characterizes the shrubsteppe. This assemblage is numerically dominated by Horned Larks *Eremophila alpestris,* Loggerhead Shrikes *Lanius ludovicianus,* Marsh Hawks, *Circus cyaneus,* Sage Thrashers *Oreoscoptes montanus,* Brewer's Sparrows *Spizella breweri,* and Sage Sparrows *Amphispiza belli,* all species which, in this region, are more or less restricted to shrubsteppe habitat types.

This analysis has revealed that a generally-defined shrubsteppe bird community can be identified, and that variations on that theme can be detected within the shrubsteppe sub-region. The observations rest on a method that lacks quantitative resolution, however, and the geographic scale is still such that substantial habitat variation may be included. In an attempt to define these apparent community patterns more precisely, we conducted a series of transect censuses (EMLEN, 1971) on 17 plots at 11 geographic locations in the shrubsteppe of southeastern Oregon during June 1977. We restricted attention to survey plots vegetationally dominated by sagebrush *(Artemisia tridentata)* or greasewood *(Sarcobatus vermiculatus)* and with more than 10% shrub coverage; the sample of plots was therefore vegetationally more homogeneous than that used in the roadside count analysis. Quantitative measures of vegetation composition and structure were made at each transect location at the time of censusing.

All 17 censuses were generally quite similar in their breeding avifaunas. Total species diversity did vary among the plots, but the only significant correlations of diversity variations were with total species number (richness) and with the densities of incidental or sporadic species. A clustering of the plots derived from their overall avifaunal similarities was subjected to discriminant function analysis, a procedure that in essence determines how accurate the clustering algorithm has been, and which variables act most forcefully to determine the patterning of plot clustering. This analysis revealed that the plot clusterings, which showed no clear relationships to underlying vegetational variations, were in fact "real", and that Brewer's Sparrow density was the first variable discriminating the plots clustered, with Sage Sparrow and Sage Thrasher densities following in the stepwise discriminant procedure. In other words, variations in the densities of Brewer's Sparrows, the numerically dominant species, made major contributions to the overall patterns of avifaunal similarities among the plots; Brewer's Sparrow densities were also significantly correlated with total community density and with species evenness. The view that emerges from these quantitative surveys, then, is one of a sub-regional shrub habitat type in which a few widespread and characteristic species dominate, leading to high plot similarity, while the variations in overall community structuring (e.g. diversity) that do occur are associated primarily with variations in species richness, due to the contributions of various "peripheral" species. The sub-regional "patterns" in community parameters may thus represent variation about a core of characteristic species that is due to the influence of species with specific but localized habitat requirements (e.g. Rock Wrens *Salpinctes obsoletus*) or stragglers from other nearby habitats; as such, the "patterns" may be more apparent than real.

If real patterns exist in breeding bird communities, one might expect to find them most evident in local breeding assemblages, for it is at this geographic scale that the competitive interactions that are presumed to produce the patterns should occur, and where close

responsiveness to environmental variations might be most evident. Our studies have included intensive population censusing in 9-ha plots during successive breeding seasons at several locations in the northwestern shrubsteppe: the results of the censuses of four plots in the Arid Lands Ecology (ALE) Reserve in southeastern Washington are depicted in Fig. 1. Several features of these community censuses merit comment: (1) The species composition of the avifaunas is quite stable, with the same three species contributing all or almost all of the breeding individuals in all plots in all years. (2) Despite this, variation in species diversity (H') is considerable (range: 0.57–1.11, Fig. 1), reflecting differences in species evenness among the samples. (3) There are considerable annual variations in the densities of the species, and in total avian density. (4) The individual census plots, located within 7 km of one another but in somewhat different expressions of the shrubsteppe habitat type, differ in absolute and relative abundances of the species.

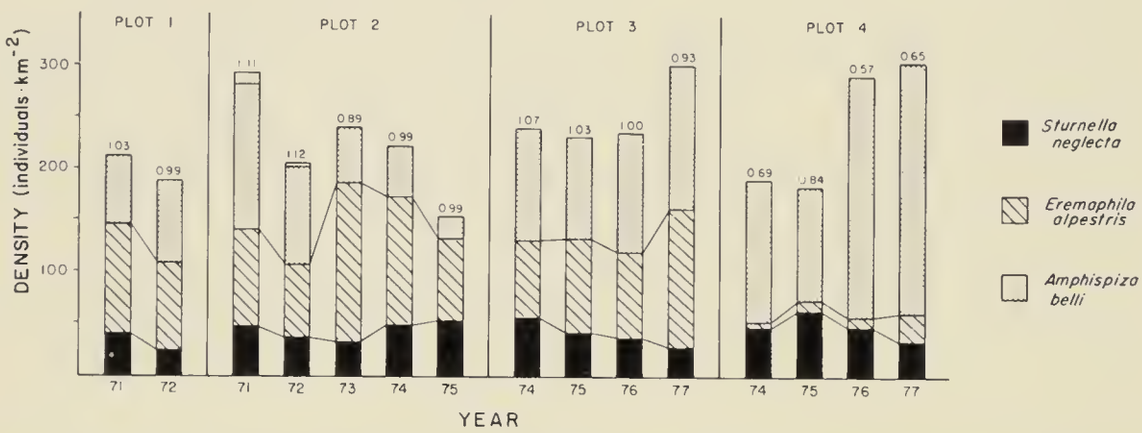

FIGURE: 1. Densities of breeding species in four 9-ha census plots at a shrubsteppe study area (ALE) in southeastern Washington. Numerals above the histograms are diversity index values(H').

At this local level of spatial resolution, then, community patterns become indistinct. The constancy in species number and composition may be taken as indicating that only a single avian community is represented, and thus only one portion of the sub-regional or regional pattern is exhibited. But the variations in species densities influence community features substantially. What value of diversity or total density, for example, should be taken to characterize this local assemblage in broader comparisons: the values from plot 4 in 1975 or in 1977, or the values of plot 2 in 1971? In another analysis (WIENS, in preparation) it has been shown that opposite trends in patterns of avian community density, biomass, diversity, etc. can be generated for study areas distributed across a precipitation gradient in the North American Great Plains depending upon which single values are taken to characterize the sites from a series of plot/year samples at each location. There, as at ALE, it appears that while species composition may be relatively stable, the details of community structuring vary so much among local sample plots and between years that definition of consistent patterns in elusive.

Community resource relationships

Community theory relates patterns in the structure of communities to competitive restraints on the resource utilization of species populations. One of the features of

community theory that makes it so difficult to test is the ever-present possibility that, no matter how many ecological variables one measures, documenting independence of community patterns or high similarities in resource utilization among the species, there may always still exist other unmeasured variables that may be critical in facilitating coexistence among potential competitors. Given this, the hypothesis that the local variations that we witness represent an ecological "fine-tuning" to local resource or environmental conditions is essentially beyond disproof. By examining some of the more obvious resource relations of these assemblages, however, we may be able to at least develop intuitions about the meaning of the local variations.

Vegetation relations

Some of the variation within and between census plots at ALE (Fig. 1) can be related to vegetational changes. The four plots differ, for example, in the coverage of sagebrush and bunchgrass (≦1%[plot 2] – 25% [plot 4] and 19% [plot 4] – 59% [plot 3], respectively), and studies at ALE (ROTENBERYY & WIENS, 1978) as well as our survey of shrubsteppe habitats in southeastern Oregon indicate a strong correlation between breeding densities of Sage Sparrows, for example, and sagebrush coverage. Further, the changes in relative abundances of the breeding species on plot 2 from 1973–1975 can be related to a range fire that swept over this plot in August 1973, reducing shrub coverage from 8% to less than 1% and leaving the vegetation dominated by *Agropyron*. The other yearly variations in species abundances on the ALE plots, however, cannot easily be associated with variations in local environmental conditions or resource levels.

Are variations in avian communities at a broader level more clearly associated with vegetation structure or composition? In our 1977 survey of southeastern Oregon, measures of some 17 vegetation variables were gathered in association with the bird censuses. Considering first relationships with single vegetation variables, Sage Sparrow density was highly correlated with sagebrush coverage, as noted above. In addition, densities of Brewer's Sparrows covaried significantly with a measure of the "robustness" of the shrubs (the proportion of the total vegetation vertical profile occuring 30–60 cm above ground), while Western Meadowlark *Sturnella neglecta* abundance was positively correlated with the occurrence of several features of grassy vegetation. Overall, however, there were few significant correlations between species' abundances or occurrences and vegetation variables, and none of the community attributes (total density, species number, diversity, evenness) was correlated with any of the vegetation variables. This suggests either that the birds have few distinct affinities for key vegetation features and do not clearly partition themselves ecologically in this dimension, that we are dealing with what the birds view as a single vegetation type and the variations we record are of little consequence to them, or that they may respond to a multiplicity of interacting vegetation variables rather than to single features. We tested this latter possibility by conducting a principal component analysis of the vegetation measures and then searching for significant relationships between the bird densities or community attributes and the newly-defined axes of the vegetation principal components. While some associations did emerge (meadowlarks, for example, exhibited a positive loading on the first vegetational principal component, which was associated with several features of grass coverage), in general there were few interpretable correlations of avian features with the multivariate vegetation

measures. The analysis suggested that variation in features of the bird communities over this sub-region is in fact ordered quite differently from that of the vegetation. This lack of a close relationship of bird densities to vegetation composition and structure is perhaps to be expected from the independence of at least some of the annual density variations at ALE (Fig. 1) from the underlying vegetation matrix.

Trophic relationships

Documenting differences in the diets of coexisting species has been a persistent focus of community studies, perhaps because of the widespread belief that food supplies are normally limited and trophic divergence is therefore necessary to reduce competition. Given the consistency in breeding species composition at local scales in the shrubsteppe and the high degree of habitat and spatial overlap among the species, we might expect consistent dietary differences to be associated with the continuing coexistence of the members of this ground-foraging guild. The studies at ALE have included repeated sampling of the species' diets (Rotenberry, 1978), and the basic pattern that emerges from these analyses is as follows. All of the species are highly insectivorous during the breeding season, concentrating on phytophagous forms (coleopterans, especially weevils, early in the season, grasshoppers in late summer). At any one point in time, the diets of different species are quite similar. A ranking of spring samples by diet similarity, for example, first lists Horned Larks and Sage Sparrows from May 1972 (99% similarity), then May 1971 Horned Larks (95%) and May 1971 Sage Sparrows (94%), then April samples of these species (92%). The ranking is on the basis of time of collection rather than species of bird. Birds of different species taken at the same times are thus eating the same things, while birds of the same species taken at different times are eating different things. There is no indication that smaller birds have more specialized diets than larger birds, as predicted by optimal foraging theory (Ellis et al., 1976).

The species breeding at ALE differ substantially in morphology (by a factor of 5 in body weights, 3 in bill lengths), and from these differences one might expect differences in the *sizes* of prey consumed. A close relationship between trophic morphology and prey size is in fact presumed in much current ecomorphological theory, although in a broad analysis of morphological variation and feeding ecology of grassland and shrupsteppe birds such relationships were conspicuously absent (Wiens & Rotenberry, MS). The samples collected at ALE indicated a high degree of overlap among the bird species in the sizes of prey they consumed (Rotenberry, 1978), with the variations in prey sizes again being associated with the time of sampling (and the proportionate contributions of seeds to the diets) rather than the species collected. The overall impression from these studies, then, is one of substantial opportunism in diets among the breeding birds: as patterns of prey availability change in time, the birds change in their prey selection, but all species apparently respond in quite similar fashions.

Conclusion

Our findings suggest that the "patterns" that characterize shrubsteppe bird communities in the Pacific Northwest exist only at a general level, being most apparent when comparisons are made between this habitat type and other regional habitats. When

assemblages are examined in more detail at sub-regional, "within-habitat" levels, the patterns become more indistinct, and are associated with the occurrence of incidental species rather than with attributes of the dominant breeding species. In other words, it becomes important to determine not just how diversity or number of species varies, but which species contribute to the community attributes. At a local level, the species composition stabilizes and the general community patterns largely erode or disappear. The breeding populations of the species vary considerably between years and plots, and the expected divergences in resource utilization between the species are consistently lacking. The patterns expected from community theory are thus evident in general qualitative features of avifaunas at a regional level but dissolve when the quantitative details of local breeding populations are considered.

To us, this failure of the "expected" community patterns or resource utilization differentials to appear at the local level is disconcerting, for if processes such as resource limitation and competition are determining the patterns one should expect to be able to document them in detailed studies of local populations, where the presumed interactions must occur. We have interpreted our results, instead, in the context of the variable, unpredictable, and at times severe nature of the climate in this region (WIENS, 1974, 1977; WIENS & ROTENBERRY, 1978; ROTENBERRY, 1978). The periodic climatic stresses may prevent local assemblages from achieving full ecological saturation and resource limitation, with the consequence that the bird populations may be effectively decoupled from close biotic interactions or control, and local variation may be substantial. The non-equilibrium status of bird assemblages throughout the northwestern shrubsteppe, combined with the general sub-regional homogeneity of the shrub desert habitat, may obviate the development of clear "within-habitat" patterns.

Of course it is possible that the variability and looseness of these shrubsteppe bird assemblages is a function of peculiarities of this particular environment, and that the patterns expected from theory may emerge elsewhere. Previous studies (WIENS, 1974; WIENS & DYER, 1976) suggest that ecological patterns in North American grassland avifaunas are also indistinct, but this is also a vegetationally simple, climatically irregular environment.

We do not know how general our view of bird communities may be, but it is apparent that our findings indicate some complications in deriving answers to the two questions posed at the outset of this paper. How can we discern the mechanism responsible for community patterns if the patterns are evidenced at a regional or between-habitat level but not locally or within habitats? What sorts of mechanisms, in fact, might be operative at broad spatial scales but not locally? Ideally we should begin to define the mechanisms through careful manipulative experiments in real-world situations. These can be accomplished (with difficulty) at a local level, where their meaning may be clouded by natural variability; at a regional level, where the patterns are more apparent, experiments cannot be conducted, and we are restricted to correlative "tests" which, of course, say little of causal mechanisms. The problem becomes one of determining the proper scale for the study of bird communities and their processes, and this scale may differ in different vegetation formations, in regions with different biogeographic histories, in avifaunas with different proportions of migratory and resident species, or in different avian guilds. The challenge of conducting serious studies of avian communities is formidable.

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Species Packing in Insectivorous Bird Communities: Density, Diversity, and Productivity

Martin L. Cody

Introduction

Beginning twenty years ago, bird ecology took dramatic new turns with the unique approaches and studies of Robert MacArthur (see Cody & Diamond, 1975 for a historical and conceptual review). MacArthur (e.g., 1965) demonstrated that bird species diversity in habitats censused within a given geographic region varies closely with simple measures of the structural aspects of vegetation. These and numerous follow-up studies (see Cody, 1974) show that around 90% of the between-habitat variance in bird diversity is attributable to differences in the structure of the habitat. This relation and its statistical qualifications bring up the following three points:

1. Bird species diversity is correlated to the foliage height diversity as measured in the original studies apparently because foliage height diversity is itself correlated to the diversity and availability of foraging sites for insectivorous birds, and to the availability of the insect food supply.

2. A more direct measure of food availability might therefore erode some of the residual 10% variance in the bird diversity - vegetation structure relation.

3. Bird diversity but not bird density is predicted by measures of vegetation structure. A direct measure of the food supply might lead to a predictive treatment of bird densities as well as fine-tune the bird diversity predictions.

A powerful start to a resource/consumer theory that incorporates both consumer diversity and density was provided also by MacArthur (1970). Now known as MacArthur's Minimization Principle, the components of the theory are a set of species' utilization functions U_i over a resource spectrum R_j, and a resource production function P; it is shown that natural selection will minimize the expression $[P - \sum_{ij} k_i U_{ij}]$ by adjusting the vector k_i of species densities and eliminating from the consumer community those species that detract from the least-squares fit of overall consumer utilization and the resource availability or production. Recently T. Case (1979, in press) has demonstrated the existence of a Liapunov Function for the theorem, and both Case and Roughgarden (unpubl.) have extended the theoretical argument.

While the development of the theory continues apace, several ambiguities remain from the point of view of field application. It is not clear, for example, whether the production function P should measure standing crop or renewal rate, or represent some aspect of both. Further, temporal variation in production, expressed perhaps as confidence limits around P, should also affect the level of species packing and the makeup of the equilibrium community, but as yet has not been incorporated into the theory. But already we have been given valuable insights by this approach into the organization of consumer communities, and it is clear that most studies to date have been negligent in measuring only species' utilization curves while ignoring resource production.

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Methodology

Since early studies on the influence of food density and competitors on wren territory size in 1970 (Cody & Cody, 1972), I have worked on a simple method for estimating the food supply of insectivorous birds. The technique is that of "stickyboards", and its use has become widespread in recent years, especially among lizard ecologists (e.g., Simon, 1975; Fuentes, 1976; Ballinger, 1977).

Insects are caught by adherence to a sticky substance, Tree Tanglefoot™, which is spread on 10 cm x 10 cm thin plastic or fiberglass plaques. The plaques are painted flat white and suspended, by a wire through a small corner hole, in the vegetation at various heights above the ground in plants of various species and foliage density characteristics. I use $^1/_2$ oz of Tanglefoot on each side of the plaque, spread smoothly; the plaques are revisited every 24 hr, the trapped insects are removed, counted and measured, and the Tanglefoot replenished as necessary.

The data on insect densities and size distributions obtained from Tanglefoot plaques are date, size, height and vegetation specific, and also provide temporal trends relative to each of these variables. In particular, these data invite comparisons between sites in different habitats, between different years in the same habitat, and between differing insect density estimates at different heights above the ground at a particular site. The data provide estimates of both standing crop and removal rate. It would be indeed foolhardy to claim that insects caught on the Tanglefoot plaques are a direct measure of the availability of insects eaten by insectivorous birds. The plaques catch mostly the more mobile Diptera, Hymenoptera and Homoptera, and other taxa as well as non-flying insects are vastly underrepresented. However, I have reason to believe that there is reasonable correlation between the numbers of trapped insects and the availability of bird food, and the moderate success of pre- and postdictions of bird density based on Tanglefoot catches (see below, in part) at least justifies further work. I have in preparation a comprehensive review of both technical aspects of the methodology and predictive aspects of bird density (Cody, 1979a), and this work may be consulted for both methodological details and further results.

Mediterranean scrub on four continents

First I compare bird and insect densities in a single habitat type, chaparral, characteristic of regions with a Mediterranean climate. A four-continent comparison treating the birds and plants of matched sites in California, Sardinia, Chile and South Africa was recently compiled (Cody & Mooney, 1979), where the matching was based primarily on climate and secondarily on plant physiognomy. Birds were censused at each (2–3 ha) site, and Tanglefoot plaques were set at all sites except in Chile; malaise traps operated in both Chile and California show that the Chilean site is very similar to California in insect density, but with a smaller spring peak in abundance and with higher mid- and late-summer counts.

In parallel with the strong similarities in vegetation structure among the four sites, the total bird diversities are very similar (as are the means and ranges of morphological and behavioral aspects of bird phenotypes represented). But bird densities differed markedly among sites, with higher densities in Chile and California (16.56 pr/ha and 14.44 pr/ha respectively), intermediate numbers in Sardinia (13.34 pr/ha) and far lower density in South Africa (9.32 pr/ha). These figures cannot be interpreted by a consideration of

vegetation structure or bird diversity, but they parallel differences in insect densities among sites as estimated by Tanglefoot plaques. The areas under graphs of insect density vs vegetation height in California, Sardinia and South Africa are respectively 198, 94, and 65. The low insect count in South Africa is in turn related to a lowered plant productivity on laterite soils (Cody & Mooney, 1979).

Arizona Pine-Oak-Juniper

Besides variation in insect density among similar habitats at different sites, insects show year-to-year variation in abundance at a given site. I have censused birds at a 2.7 ha site in the Chiricahua Mts of southeastern Arizona intermittently since 1966, and have in recent years trapped insects in this habitat with Tanglefoot plaques (Cody, 1979b). At this site, as with most areas in the southwestern United States with less than 75 cm of annual precipitation, the spring and summer insect catches reflect the amount of precipitation in the preceding 12 months. For the years 1973, 1974, 1975, 1976, the rainfall at the site was 152%, 49%, 84% and 94% respectively of the long-term average of 51.3 cm. The insect catches parallel these figures very closely: 19.4, 2.4, 15.0 and 16.5 respectively (first-day catches, total insects caught/plaque side/24 hrs).

The composition of the bird community at the site changes with the precipitation and the density of insects. Of the 20 species present in the pre-drought years before 1974, 8 were absent in 1974 and an additional 5 species were present. The 8 absentees were all species characteristic of more mesic habitat either at higher elevation or in riparian sites, while the 5 newcomers were species characteristic of drier mesquite scrub habitat at lower elevation. The post-drought recovery of the bird community matched the increasing insect catches, and by 1976 6 of the 8 drought-sensitive species had been regained, and 2 of the 5 beneficiaries of the drier seasons had been lost. Note that in drier seasons the structure of the vegetation is unchanged; here diversity has a direct relation to the site productivity.

Öland Juniper-Oak scrub-woodland

Bird density and diversity are determined by the way in which species' utilization curves are best fit or assembled to the resource production curve. As the best estimator of bird utilization I use the distribution over height of bird foraging times; such curves may be combined over different species as long as the sizes and foraging behavior of birds are similar. To estimate a production curve P one might use the distribution over height of vegetation density, which provides the substrate on or from which insectivorous birds forage, or the distribution over height of Tanglefoot insect catches, a more direct measure of food availability, or some combination of the two.

The match of bird foraging height distributions to vegetation and insect denties is illustrated by the sylviid warbler assemblages at Bejershamn on the island of Öland (Cody, 1978). This site has a range of habitat from low and open *Juniperus-Rosa* heath through low *Populus-Alnus* to oak woodland. In simple and lower habitat monopolized by *Sylvia nisoria,* the foraging height distribution of this species is a close match to the distribution of vegetation density (Fig. 1a). In taller habitat, in which the species combination *S. borin* + *S. curruca* (Fig. 1b) is found, the utilization curve of the two-warbler combination is a compromise between vegetation density which peaks below maximum warbler utilization

and insect density which peaks above. Thus it appears that high vegetation density and high insect density both attract foraging warblers, and are both exploited as if they are independent components of food availability.

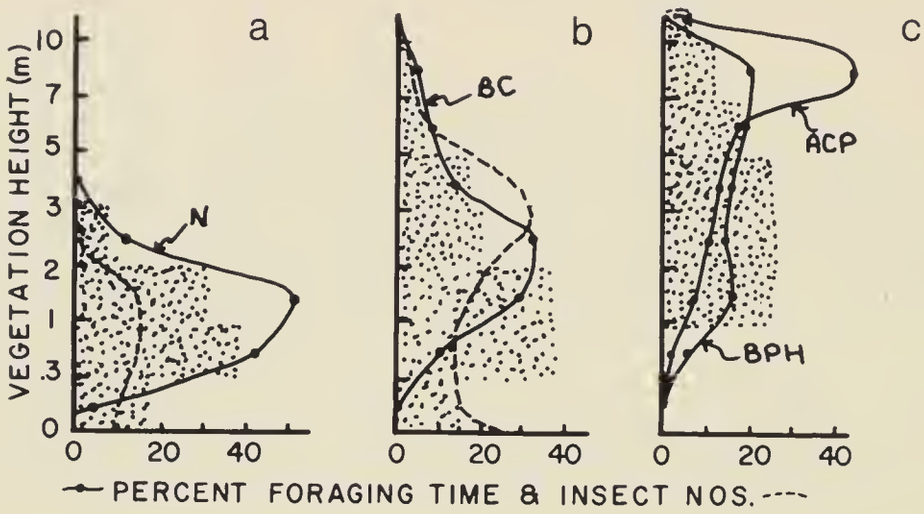

FIGURE 1. Vegetation density (stippled histogram), insect density (dashed line) and foraging height distributions of warblers or warbler combinations. Data collected at Bejershamn, Sweden (see text). Warbler species represented are *Sylvia nisoria* (N), *S. borin* (B), *S. curruca* (C), *S. atricapilla* (A), *Hippolais icterina* (H) and *Phylloscopus trochilus* (P).

The matching of warbler foraging distributions to vegetation and insect density profiles forms the basis of determining which warbler assemblages are viable and stable in which habitat type. In Figure 1c the utilization curve of the commonest 3-species warbler combination BPH *(borin-P. trochilus-H. icterina)* is illustrated against the background of its average vegetation profile; an alternative combination ACP *atricapilla-curruca-P. trochilus)* is rarely observed, and provides a much poorer match to vegetation (here insect data are not included).

Maquis, Middle Atlas near Beni Mellal, Morocco

The question as to whether the vegetation density profile or the insect density profile provides the best estimator was addressed in recent studies in Morocco. Near Beni Mellal in the Middle Atlas Mountains a hillside with a uniform NW exposure was censused at four sites: at 800 m in an open, multilayer *Pistacea-Ceratonia-Euphorbia* formation, at 1000 m in mixed *Ceratonia-Arbutus-Juniperus,* at 1200 m in dense chaparral of *Arbutus-Phyllarea-Quercus,* and at 1400 m in a closed-canopy monolayer of *Quercus ilex.* The vegetation height (see Table 1 and Fig. 2) changes little over this gradient (from 4.85 m at the bottom to 5.15 m at the top of the hill), but the vegetation profile changes to increasing density higher off the ground with higher elevation (Table 1). The areas under the foliage profiles A_D are likewise similar; Tanglefoot insect catches, however, show that the lowest site is lowest in insect density (area under graph of insect x height, $A_I = 37.8$), the second-highest site has highest insect densities ($A_I = 101.4$), with intermediate figures for the highest and second-lowest sites. The profiles of vegetation and insect densities are given in Figure 2.

TABLE 1. Summary statistics of four maquis sites on a Middle Atlas hillside near Beni Mellal, Morocco.

	top 1400 m	one down 1200 m	one up 1000 m	bottom 800 m
Vegetation height (m)	5.15	5.00	4.09	4.85
Vegetation half-ht (m) [1]	2.15	1.18	1.39	0.42
Habitat gradient H [2] (m)	5.32	4.36	3.88	3.73
Vegetation density A_D [3]	17.6	19.3	18.4	23.9
Insect density A_I [3]	81.0	101.4	75.9	37.8
COV(A_D, A_I)	0.115	0.110	0.085	0.083
Total no. species	26	24	17	15
Pr/ha (all species)	13.43	16.75	14.78	12.33
Pr/ha (insectivores)	9.90	13.53	10.70	8.18

[1] Height at which half total vegetation density is above and half below.
[2] H is a principal component ordination of habitat based on the vegetation profile.
[3] A_D and A_I are the areas under plots of vegetation and insect density respectively versus height (see Fig. 2).

With increasing equitability of the distribution of vegetation in the foliage profile from the bottom of the hill to the top, bird species diversity likewise increases (Table 2), from 15 species at the lowest elevation to 26 species at the highest. A total of 33 species is found in the four sites, and species turnover with changing vegetation structure is smooth and continuous with the single exception of *Parus major*'s absence (# 10) at the second site up.

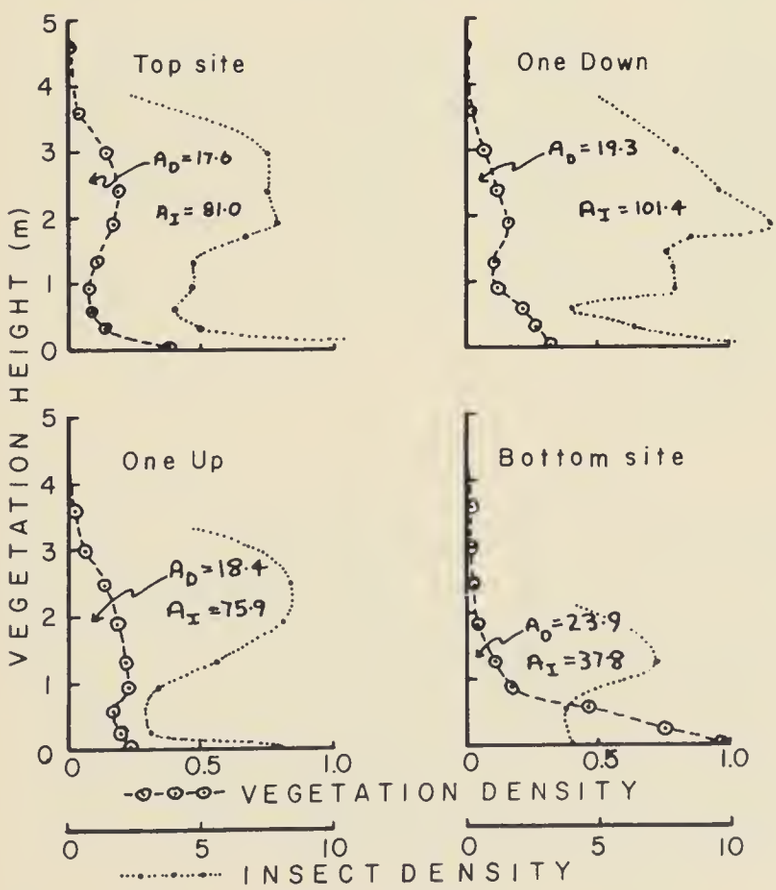

FIGURE 2. Vegetation density profiles and insect density profiles of four sites at different elevations on a hillside south of Beni Mellal, Middle Atlas Mountains, Morocco. The areas under each curve are given. Note that the congruence between the insect and vegetation profiles is high at the Top Site, lowest at the Bottom Site, intermediate elsewhere. See text for discussion.

Bird density does not parallel the trend of bird diversity, however, and maximum density of 16.75 pr/ha is found at the second highest site, minimum density of 12.33 pr/ha

TABLE 2: Densities of bird species (pr/ac) censused at four sites on a hillside in the Middle Atlas Mts of Morocco south of Beni Mellal.

	Species censused:	bottom site	one up	one down	top site
33	*Pyrrhocorax pyrrhocorax*				+
	Columba palumbus				0.14
	Garrulus glandarius				0.19
30	*Parus caeruleus*				0.27
	Oriolus oriolus			0.14	0.27
	Pica pica			+	++
	Parus ater			0.18	0.27
	Coccothraustes coccothraustes			0.09	0.18
25	*Fringilla coelebs*			0.46	0.45
	Muscicapa striata			0.18	0.15
	Phylloscopus bonelli			0.23	0.18
	Cuculus canorus		+	+	+
	Erithacus rubecula		0.37	0.55	0.64
20	*Chloris chloris*		0.12	0.27	0.09
	Sylvia atricapilla		0.75	0.64	0.14
	Regulus ignicapillus		0.37	0.18	+
	Luscinia megarhynchos		0.60	0.64	–
	Hippolais polyglotta		0.18	0.06	+
15	*Sylvia cantillans*	0.44	0.48	0.64	0.64
	Turdus merula	0.17	0.37	0.46	0.45
	Troglodytes troglodytes	0.17	0.60	0.27	0.41
	Streptopelia turtur	0.53	0.75	0.36	0.32
	Alectoris barbara	0.28	0.24	0.27	0.09
10	*Parus major*	0.17	–	0.27	0.18
	Pycnonotus africanus	0.28	0.48	+	0.14
	Serinus serinus	0.35	0.12	0.27	0.14
	Carduelis carduelis	0.35	0.24	0.27	0.09
	Sylvia melanocephala	1.25	0.24	0.27	
5	*Emberiza cia*	0.53			
	Emberiza calandra	0.09			
	Monticola solitarius	0.09			
	Oenanthe hispanica	0.23			
1	*Corvus monedula*	+			

is found at the bottom site, with intermediate bird densities at the remaining two sites (see Table 1). Thus the differences in bird densities parallel the differences in insect densities among sites. Although statistics are not possible here, the introduction of a second independent variable, the covariance between vegetation and insect densities, COV (A_D,A_I), helps to explain the (dependent) bird densities in an interesting way. I define COV (A_DA_I) as $A^2_{D,I}/A_D.A_I$, the square of the area under the product of the vegetation and insect density curves divided by the product of each curve's area. Thus the covariance index is low when vegetation and insect densities peak at different heights, and is maximum when the two curves are congruent. The covariance terms enters into an equation for bird density with a negative coefficient, which at first thought is rather surprising. I interpret this negative coefficient to indicate that high vegetation density and high insect density can

be treated as at least partially independent resources for the insectivorous birds; the higher bird densities are found in those habitats in which the vegetation and insect density curves are disjunct, in which some bird species adjust their foraging height more to the vegetation density spectrum, and other species more to the insect density spectrum. More work is required before the interaction between these two potential resources and its effect on bird densities becomes well understood.

Conclusions

The studies summarized here give rise to the following tentative conclusions.

1. More accurate bird diversity and especially density predictions are possible by incorporating crude estimates of insect densities obtained by stickyboard methods.
2. Bird diversity is mainly determined by the distribution over height of vegetation density, whereas bird density is mainly determined by the abundance over height of the insect food upply.
3. Species packing in insectivorous bird communities is determined via a minimization principle such that the combined foraging height distributions of the insectivore community match some combination of the distributions of foraging substrate as measured by the vegetation profile and the insect availability as measured by Tanglefoot insect catches.
4. The spectra of vegetation density and insect density over height within the habitat interact in non-trivial ways to affect bird density; maximum bird density is found where the two spectra are disjunct, indicating some independence in their effects on the bird consumers.
5. Community organization may appear low in predictability, or chaotic, for two obvious reasons. One is the existence of close ecological homologues, competitor species that interact directly over territory; the second is that environmental variability, especially in the insect food supply and especially within a habitat between different years, generates a different community structure. Once these factors are understood and measured, much of the apparent chaos vanishes, and the result of selection for a matching of consumers to resource range, productivity and variability, can be demonstrated.

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Avifaunistic Enrichment and Bird Community Saturation

Staffan Ulfstrand

It is often said that bird communities on continents are saturated and that the number of species of any particular community is in equilibrium because any further increase in species richness is prevented or at least greatly delayed owing to the opposition that invaders encounter from the co-adapted set of species already present. If this is strictly true, and since a given fauna of course is no more than the total sum of its component communities, faunal enrichment should be a rare event. My point is that, judging from what is going on in Northern Europe, it is not. On the contrary, there is a continuing avifaunal enrichment. Can this fact be reconciled with the notion of community saturation and stability? This question will be briefly discussed in this paper. Although examples are taken from Sweden and other Scandinavian areas, I believe that the situation is representative for many parts of the world, where man is having a strong impact on environmental conditions.

The newcomers

As amply documented in ornithological literature, new bird species are being added to the list of breeding birds of Sweden (or any other region in Northern Europe) at a considerable rate. Does this mean that new species have been, and are, able to squeeze into existing communities, or do the new species occupy habitats newly created or heavily modified by man?

Many of the newcomers in the Swedish avifauna fall into one of the following categories:

(A) 19th century invaders breeding in eutrophic lakes, e.g. Great Crested Grebe *Podiceps cristatus*, Slavonian Grebe *P. auritus*, Shoveler *Anas clypeata*, Tufted Duck *Aythya fuligula*, Coot *Fulica atra*, and Blackheaded Gull *Larus ridibundus*.

(B) 20th century invaders of areas of regrowth, where short grass swards are being replaced by tall grass and herbs and shrubbery because of discontinued grazing by livestock, e.g. Penduline Tit *Remiz pendulinus*, Grasshopper Warbler *Locustella naevia*, Marsh Warbler *Acrocephalus palustris*, and Scarlet Grosbeak *Carpodacus erythrinus*.

(C) Birds able to exploit urban and/or extreme agricultural environments, e.g. Crested Lark *Galerida cristata*, Black Redstart *Phoenicurus ochruros*, Corn Bunting *Emberiza calandra*, and Collared Dove *Streptopelia decaocto*.

These examples show that newcomers most often settled in habitats that were or are being heavily affected by man's activities. The 19th century was an epoque of lake and marsh draining (e.g. Wolf, 1956), and while many rich bird localities no doubt were destroyed in the process, a large number were also created, when the water level of lakes was lowered so that aquatic vegetation could expand. Several of Scandinavia's most famous water bird localities have such an origin. In addition, organic pollution was becoming prevalent in those days, initially increasing the productivity of aquatic ecosystems. It seems almost certain that a profound alteration of wetlands and lakes due to human

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interference was a very important circumstance granting entrance into Scandinavia to what was virtually a whole new bird community.

Similarly, changing livestock management practices resulted in a great expansion of tall ground vegetation, especially in many moist habitats, and this habitat change allowed the invasion into Sweden of a number of new species (cf. Ahlén, 1965, 1966). Urban, semiurban and agricultural environments also have expanded and changed drastically during the past centuries and provided opportunities for the advent of new species (cf. Tomialojc & Profus, 1977; Hohtola, 1978).

It appears then that most of the newcomers did not intrude into relatively stable habitats under competition with species already present, but settled in habitats that either had scarcely existed before, or else had recently expanded greatly. In no case is there any indication of a newcoming species outcompeting one present previously. Losses or decreases, which have of course also occurred in the Swedish avifauna but are not the subject of this paper, in no case can be ascribed to competition from newcomers. In addition to the creation of new habitats man's increased input of energy into many ecosystems may favour certain bird species able to live in highly modified landscapes.

Expanding species

The newcomers are but a small proportion of the total Swedish avifauna. A quantitatively more important process therefore is the large-scale increase among a considerable number of more or less abundant species, as has been documented in Finland (Järvinen & Väisänen, 1977) and almost certainly has taken place in Sweden too, although there is little evidence to rely upon. How have such expansions affected bird communities?

Although the answer in many cases is uncertain, the general rule appears to be that expansions generally have taken place in newly arisen or highly modified habitats. Sprawling reedbeds and shrubberies offer suitable habitat for, e.g., Redwing *Turdus iliacus*, Thrush Nightingale *Luscinia luscinia*, Reed Warbler *Acrocephalus scirpaceus*, Sedge Warbler *A. schoenobaenus*, Bittern *Botaurus stellaris*, and Grey Lag Goose *Anser anser*. Coniferous plantations have encouraged the expansion of Hedge Sparrow *Prunella modularis* and Crested Tit *Parus cristatus*. In a number of cases, population increases and expansions can be interpreted as recuperations after previous declines due to persecution or environmental poisoning, e.g. Razorbill *Alca torda*, Guillemot *Uria aalge*, Eider *Somateria mollissima*, Rook *Corvus frugilegus*, and Raven *C. corax*.

There is no evidence that any of these expansions have involved serious declines in closely related species. They seem to have taken place with little competitive strife. Expansions have been possible because man-made landscapes offer improved opportunities for many species, presumably in terms of access to more abundant food resources. Not only its increased productivity, but also its changing configuration may make the heavily exploited landscape favourable for many bird species. For example, habitat fragmentation and the ensuing increase in amount of habitat edge per unit area represent changes favourable to numerous bird species (cf. Lindquist, 1931; Brinck, 1966; Löppenthin, 1967). It has recently been suggested that a moderate rate of perturbation *per se* will result in higher species richness than very stable conditions (Connell, 1978). The avifaunistic changes taking place in Northern Europe seem, at least superficially, to support this notion.

Improving survival in winter quarters

It is of interest to note that all four species of birds of prey that have increased more or less continuously over a considerable period of time are long-range migrants wintering around the Mediterranean or in the tropics, viz. Osprey *Pandion haliaetus,* Black Kite *Milvus migrans,* Marsh Harrier *Circus aeruginosus,* and Montagu's Harrier *C. pygargus* (the last-mentioned was a new-comer in the past century but has still only a small population); one could probably also add the Honey Buzzard *Pernis apivorus* to this list. Also among other groups tropical or subtropical migrants figure so prominently that one is prompted to suggest that the landscape transformation currently occurring in those regions may favour the Palearctic migrants, perhaps at the expense of locally breeding species. If this is so, it would suggest that many temperate bird populations in fact are limited by conditions in the winter quarters rather than in the breeding areas. This must clearly have a considerable bearing upon the interpretation of competition studies carried out during the birds' breeding season (cf. Rappole, 1974; Ulfstrand & Alerstam, 1977).

The success of passerines

On the average, passerine species are more successful than nonpasserines. Out of approx. 100 breeding passerines, I have classified only 5 as going down, while 27 are going up. Among approx. 140 nonpasserines, 31 are going, or have gone, down and 39 up. Not one passerine species has vanished from Sweden since the commencement of ornithological activities, as opposed to 6 or 7 nonpasserines. Among some 35 species with less than 100 breeding pairs in Sweden, 22 are nonpasserines and 13 passerines, while all 26 species with more than 10^6 pairs are passerines. Two species, viz. Willow Warbler *Phylloscopus trochilus* and Chaffinch *Fringilla coelebs,* are estimated to exceed 10^7 pairs. The total number of breeding birds in Sweden is in the order of 10^8 pairs, divided among some 240 species. While passerines make up somewhat over 40% of the species, they represent over 90% of the individuals (Ulfstrand & Högstedt, 1976).

Thus, passerines make up a growing proportion of the total avifauna. Their present success must find an explanation at the community level.

Conclusions

My conclusions are that Sweden, which in this respect may be representative for much of Northern Europe, at present enjoys an avifauna richer in species and possibly also in individuals than has been the case for centuries. The increase is due to many factors, such as man's creation of new habitats, man's raising of the productivity of many ecosystems, modification of the vegetation with increased edge formation, and perhaps man's continuing perturbation of the environment. It does not seem probable on present evidence that communities used to be greatly undersaturated and that the recent increase can be regarded as a process of filling up of niche space previously under-utilized. However, whether communities are or are not saturated at some particular point in time is extremely difficult to prove. Although the faunal enrichment seems to have been possible mainly due to new or modified habitats and/or resources becoming available, there are other types of indications that temperate communities may not be strictly saturated. The fact that the provision of nest boxes has been found to have no discernible effect on other

populations than those of the hole nesters themselves (Enemar & Sjöstrand, 1972) may suggest that there are food resources not being harvested and that, thus, the community has been undersaturated, at least in a certain sense. Perhaps winter conditions keep many migratory populations breeding in the temperate region under saturation levels. Clearly the question of saturation and competition in communities existing in disturbed habitats merits further study. Habitats and hence communities in regions such as Northern Europe are in a state of continuing perturbation, and it is a source of wonder as well as a challenge for further research that man's profound transformation of the environment so far has had such a positive effect of avifaunistic enrichment.

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Seasonal Patterns in Bird Community Organization. Local and Global approaches

Carlos M. Herrera

Introduction

Birds are perhaps the group for which so far most information on community ecology has been gathered. However, most studies on bird communities have been carried out during the breeding season (see MacArthur, 1971; Cody, 1974, for reviews). The understanding of bird communities has proceeded by means of intensive study of local communities or guilds at fixed points in time, usually the breeding season, and by comparisons involving the variation of some environmental variable. All these studies have served to outline the main features of bird community patterns, but the states previous and subsequent to the breeding season have generally been ignored. This fact has been pointed out by several authors who have advocated, although apparently with little success, a wider scope in bird community studies (e. g. Recher, 1966; Fretwell, 1972; Baker & Baker, 1973).

My contribution has two aims: first to call attention to the significance of considering bird communities as dynamic entities, and its implications for our present knowledge of community patterns; and second to outline two possible approaches which may be used in studying their temporal organization.

Seasonal organization and environmental heterogeneity: the global approach

Bird communities undergo conspicuous seasonal changes, mainly in temperate areas, but also in tropical regions. These changes affect the number and identity of the species present at a given time, as well as the total abundance. For bird populations which move seasonally from one area to another the environment is made up of disjunct patches, of which a variable number are visited sequentally during the life-span of an individual. In nature patchiness in revealed in a nearly endless spectrum of spatial scales and serious problems arise when one tries to obtain any operationally useful definition (Wiens, 1976). Considering patchiness scales only on the basis of the distance between the extreme geographical areas a given population inhabits along a yearly cycle, birds as a group have evolved the ability to exploit patchy systems on much larger spatial scales than less mobile vertebrates. The full spectrum of spatio-temporal strategies (from seasonal shifts in foraging microhabitat to intercontinental migrations) may be seen as a set of responses to spatio-temporal patchiness on scales of various sizes (e.g. Hartley, 1953; Stallcup, 1968; Moreau, 1972).

Despite the obvious heterogeneity of natural systems, most of the models which are the theoretical basis of population biology and ecology deal with populations existing in single points in time and space. Only in relatively recent years have ecological studies begun seriously to consider the fundamental importance of spatial heterogeneity (see reviews in Levin, 1976a; Wiens, 1976). Thus, the prevailing consideration of bird communities at fixed points in time, which I stressed in the introduction, has to a large extent been

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simultaneous with the development of an ecological theory, largely based on Lotka-Volterra-type models, in which there was no room for the possible effects of the spatial structure of the environment.

Most theoretical treatments considering the effects of spatio-temporal heterogeneity have focused on the parameters describing the whole system within which the environmental patterning is contained (e.g. stability, diversity). This approach provides us with a view of the system from outside its boundaries, and it may properly be called a' global approach.

Theoretical and empirical results obtained so far have shown that consideration of spatial effects may substantially change our understanding of the organization of ecological communities. The potential for coexistence and specific interactions is altered by spatio-temporal heterogeneity coupled with dispersal and migratory ability. The spatial aspect of the environment, by means of opportunities for movement and habitat diversification, makes possible the coexistence of species which could not otherwise survive together (e.g. LEVIN, 1974, 1976b; SLATKIN, 1974; LUCKINBILL, 1974).

LEVIN (1976a, b) attempted to catalogue some of the ways by means of which space serves to facilitate coexistence and, in general, to increase diversity. He classified them as due to 'local uniqueness', 'phase differences' and/or 'dispersal'. In the case of bird communities, the effects on community structure of the 'local uniqueness' are reasonably well known when the other two factors are left aside and fixed-time approaches are used. In stationary breeding communities, patterns of within-habitat species diversity are affected by spatial heterogeneity in the form of habitat complexity (MACARTHUR & MACARTHUR, 1961; KARR & ROTH, 1971; BLONDEL et al., 1973). Between-habitat diversity is another effect of spatial patterning on community diversity (ORIANS, 1969; JÄRVINEN & VÄISÄNEN, 1973, 1976).

The analysis of seasonal organization of bird communities inevitably introduces, simultaneously, the other two fundamental aspects of heterogeneity, namely 'phase differences' and 'dispersal'. Migration between areas and seasonal shifts in microhabitat both imply the sequential exploitation of two or more environmental patches of which the profitability is phase-differentiated, the new patches tending to be more heavily exploited at the same time as the preceding one becomes unprofitable and/or the new one increases its relative profitability. Furthermore, the successive exploitation of several phase-differentiated patches involves an ability to move across the intervening space. This is precisely the third of LEVIN's components outlined above.

Accordingly, the study of seasonal organization of bird communities involves the consideration of all the three factors by means of which heterogeneity facilitates coexistence. For this reason, bird communities are a good, albeit complex, study system for the investigation of the effects of environmental patterning on community structure and for testing predictions emanating from theoretical models which consider environmental heterogeneity. In practice, however, extensive information on sub-system parameters (inter-patch migration rates, population densities within every patch, etc.) is needed to test model predictions. This kind of information is virtually nonexistent even for relatively small areas, mainly because of insuperable difficulties in defining patches, so a global approach to the study of temporal organization of bird communities is still far from possible, at least in a way which is congruent with the theoretical models built so far. The

first, enormous task would be to get a meaningful criterion for recognizing patches in a widely applicable sense. This, I feel, is a philosophical rather than ecological problem which will continue to disturb researchers for many years.

Fixed space and variable time: the local approach

Another approach to the study of seasonal organization would be to study the system from the inside, the observer transcending its boundaries and placing himself within a given patch where he could follow changes in the local community structure in the course of time. This we could call a local approach.

The simplest way is to follow through time the ecological parameters which have ordinarily been used to assess structure in fixed-time contexts, such as, for example, diversity, patterns of resource partitioning, etc. Many authors have analysed seasonal changes in species diversity and total abundance (e.g. Blondel, 1969; Beals, 1970; Holmes & Sturges, 1975; Raitt & Pimm, 1976) but, on the other hand, changes in niche breadth and overlap, and patterns of resource use, have hardly been dealt with (but see e.g. Crome, 1975; Feinsinger, 1976; Herrera, 1977; Ulfstrand, 1977). In this context, it is interesting to consider the following: to what extent do the parameters describing local community structure at a given time depend on present environmental conditions, and to what degree do they also depend on past events or conditions within or outside the habitat? One may distinguish two groups of community parameters, depending on whether or not they 'track' the environmental conditions through time.

Community parameters 'tracking' environmental conditions through time

Most studies have firmly established that at any given time in the annual cycle, some descriptive parameters (species diversity, population sizes) are closely tied to resource availability in the habitat at that time (e.g. Blondel, 1969; Holmes & Sturges, 1975; Raitt & Pimm, 1976). Furthermore, adjustments to present conditions by means of alterations in resource partitioning patterns have been demonstrated in some instances (Feinsinger, 1976; Wolf et al., 1976; Herrera, 1978b), related to resource availability changes. Thus, in some of its gross descriptive parameters, successive temporary states of a local bird community are adjusted to present environmental conditions, 'tracking' it through time. As some of the results obtained in fixed-space, variable-time contexts are equivalent to some of those commonly arrived at in fixed-time, variable-space contexts, then the proposal of some kind of equivalence between time and space could be justifiable. In this case, the study of seasonal organization of local bird communities would not add any substantially new element to our present knowledge. However, as shown below, there are some community parameters which do not 'track' environmental conditions through time.

Community parameters not 'tracking' environmental conditions through time

Two groups of such parameters can be distinguished, which relate, respectively, to the community as a whole and to the individual species. I shall deal with the former group first.

It has been generally accepted by most authors that nonresident species periodically invading a community exploit a surplus of resources which local residents are not able to monopolize. Analysing the distribution pattern of European, long-distance migrant passerines, I have shown elsewhere (HERRERA, 1978a) that the percentage of individuals in terrestrial, breeding communities is negatively correlated with the mean temperature of the coldest month. The latter must be closely related to the unfavourableness of the adverse season to resident populations, which must impose a 'bottleneck' on the 'flow' of resident populations from summer to summer. Accordingly, the resident sector of the community acts throughout the yearly cycle as a 'carrier' of information on past circumstances in the habitat and this information influences future community states. In this way, local community structure at a given time (e.g. breeding season) depends not only on present conditions but also on past environmental features.

Within a particular guild which exploits a kind of resource of intermediate seasonality, the acquisition of resident status implies the monopolization throughout the annual cycle of a certain fraction of total resources, from which nonresidents were excluded in ecological or evolutionary time, or are still actively being excluded. Evidence exists demonstrating a competitive superiority of residents over nonresidents in exploitative and interference terms (WILLIS, 1966; FEINSINGER, 1976; WOLF et al., 1976; COX, 1968). The likely inferiority of nonresidents is shown also by their occupation of marginal, secondary habitats in the tropics, where they are apparently excluded from low-seasonality, primary habitats saturated with resident populations (e.g. BROSSET, 1968; LECK, 1972; TRAMER, 1974; CHIPLEY, 1976). Apparently, thus, resident species have, or have had, some kind of superiority over nonresidents, having a dominant role in guild and community organization. This aspect reveals, again, that the configuration of either a guild or community observed at a given point in time does not depend totally on the environmental conditions prevailing during that period.

As pointed out above, there are some 'not-tracking' parameters which are related to individual species. Population sizes of breeding species which migrate from a study area can be seriously affected by events occurring outside local boundaries. Climatic deterioration, habitat destruction, and exposure to toxic residues on their wintering and migratory grounds may have a substantial effect on breeding populations of several European and American passerine species (FRETWELL, 1972; BERTHOLD, 1973; WINSTANLEY et al., 1974). If, as some have argued (LACK, 1966; FRETWELL, 1972; SLAGSVOLD, 1975), it is likely that most bird species are regulated, at least in part, during the winter season, community structure and intensity of interspecific interactions in breeding bird communities could bear only a partial relationship to actual spring conditions.

The morphological configuration of local breeding communities has usually been interpreted in terms of the competitive pressures supposed to have been operating during that period. However, this may be not so in some instances. The marked pattern of morphological differentiation in feeding structures characteristic of shorebirds has been shown to promote a clear-cut ecological segregation during migration and winter periods (e.g. EHLERT, 1964; RECHER, 1966) but, on the other hand, interspecies segregation on breeding grounds is mainly achieved by means of habitat selection and range differences and, in some cases, species coexisting locally overlap extensively in resource use (HOLMES & PITELKA, 1968; BAKER & BAKER, 1973). One possible conclusion is that among

shorebirds, competitive interactions in their migratory and winter quarters may be, with respect to diversification of foraging structures, as important as or more important than those prevailing on breeding grounds (Recher, 1966; Holmes & Pitelka, 1968; Baker & Baker, 1973). As morphological features remain unchanged throughout the annual cycle, the morphological configuration of a bird community at a given time is, at least in part, the result of processes operating in other periods and/or regions.

Concluding Comments

The existence of seasonal changes in the parameters describing local communities may be seen as the manifestation, on a point-like scale, of a certain number of population processes in response to spatio-temporal patterning of the environment. We can look at seasonal alterations by having, as a background, a theoretical framework composed of models designed to handle the spatial heterogeneity of the environment, and make use of the language and concepts emanating from this new generation of heterogeneity-conscious models, in a way paralleling the fruitful use of Lotka-Volterra-type models in conventional bird community investigations. However, in practice, many difficulties arise when basic concepts have to be transferred from models to the field. Despite this formidable barrier, the global approach is potentially feasible and it represents a serious challenge which must be taken up if a complete understanding of bird communities is to be achieved.

Since the structure of a community at a given time of the annual cycle is not fully determined by the prevailing conditions at that time, it is necessary to develop a much wider concept of community than the usual one of a quasi-static assemblage. Local, successive temporary aggregations of species are neither fully independent nor totally dependent on each other. Do we, then, have many different temporary forms of a unique community or, on the contrary, do we have many different communities replacing each other throughout the year in the same location? An adequate answer to this question requires both a broadening of the concept of community and a wider temporal scope in bird community studies. At the very least, I can conclude that the consideration of seasonal organization of bird communities is a most important aspect and that it deserves much more attention than it has received so far.

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Concluding Comments: Are Bird Communities Real?

John A. Wiens

The papers presented in this symposium profile the diversity that characterizes contemporary studies of avian communities. The focus of these studies ranges from local populations to global overviews, and the conceptual foundation is energetics in some cases, competition in others, overwhelming variability in still others. These divergences reflect differences in the level of approach, in the systems studied, and, perhaps most importantly, differences in the initial conception of what is important about the system, what merits our attention. But it is becoming apparent that the pictures of bird communities that we have created are not as clearly defined as we first thought. Several factors are contributing to the increasing fuzziness of our conceptions, and these must become new foci of future community studies:

1. The reponses of birds to variations in their environments are clouded by various time lags, many of them associated with the remarkable learning capacities of birds. Site tenacity, for example, may contribute to stability in populations over several years in the face of changing habitat conditions, and learning of localized feeding customs may produce unique patterns of resource utilization that differ among local populations of a species quite independently of their community context.

2. The community patterns that we seek to define vary over a wide array of temporal scales, such as tidal cycles, breeding/non-breeding seasons, years, decades, and so on. How do we select the appropriate scale in this spectrum on which to gauge bird community organization?

3. In a like manner, we may consider bird communities over a variety of spatial scales, from individual territories and space-use foci through regional and continental avifaunas. Which of these scales is proper for seeking understanding of communities?

4. Because we are uncertain about the influences of time lags and the appropriateness of the temporal and spatial scales on which we view communities, we generally can only draw crude inferences about whether the communities are in equilibrium or not. Do biotic interactions produce the patterns that we think are real, or are the organisms decoupled from direct biotic interactions such as competition, and perhaps responsive instead to various abiotic influences? We have generally presumed the former, but that does not make it correct.

5. Finally, we must consider the prospect that bird communities may not really exist at all, in any functional biological sense. While birds are unique creatures in a variety of respects, there may be few compelling reasons to believe that their assemblages are structured independently of those of consumers belonging to other taxa that use the same resources. Workers in southwestern United States deserts, for example, have evidence that suggests that birds, harvester ants, and heteromyid rodents may collectively interact in relation to the seed resources they utilize, and that consideration of any one of these taxonomic groups by itself would lead to incomplete conclusions. We do not know how

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widespread such intertaxa interactions may be, but by constraining our studies of bird communities over the past decades with such a strong taxonomic bias, we may well have produced a perception of community organization that bears a closer resemblance to science fiction than science fact. MACARTHUR's definition of a community as any set of organisms living near each other and about which it is interesting to talk may have provided a comfortable rationale for avian community studies, but it has little inherent biological meaning. We rarely know (or seem to care) whether there are any sorts of natural boundaries about the communities we study, whether there are any discontinuities in biological processes that might act to define a functionally interrelated assemblage of organisms in which we might really expect patterns of organization to have some adaptive significance.

What, then, must we do? I submit that we must turn our attention to more intensive, long-term studies of defined local populations and environments, in relation to defined (and measured) resource bases. If assemblages of organisms are not just haphazard they must result from the operation of biotic processes. and these are expressed through individuals and populations. Only by first looking there, and then by attempting to tease apart the real from the spurious processes with manipulative field experiments, may we determine whether bird communities are biologically real, and if so whether there are "rules" governing their structure.

SYMPOSIUM ON
BIOLOGY OF NECTAR FEEDING BIRDS

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Energetics of Resource Defense: An Experimental Approach

Paul W. Ewald

Territoriality has been a focal point of intense interest throughout this century because it is often a fundamental aspect of social structure (e.g. Howard, 1920; Huxley, 1934; Lorenz, 1963). Brown (1964) provided a general explanation for the existence of territorial behavior by introducing the concept of resource defendability. This concept predicts that territoriality should occur when fitness benefits from territoriality are greater than costs.

Introductory studies of territorial behavior of nectarivorous birds applied the concept of defendability in a qualitative sense (Stiles & Wolf, 1970; Wolf, 1970). Laboratory measurements of oxygen consumption (Berger & Hart, 1972; Lasiewski, 1963; Pearson, 1950) permitted quantified descriptions of how territory owners allocate their caloric resources between various activities (Carpenter & Macmillen, 1976a; Pearson, 1954; Stiles, 1971; Wolf & Hainsworth, 1971). These quantifications formed a base for subsequent studies in which territory size and the existence of territoriality were correlated with an owner's balance of territorial gains and losses (Gass et al., 1976; Gill & Wolf, 1975). When calculations showed that territorial behavior would not increase an individual's net energy gain, territoriality was generally absent (Carpenter & Macmillen, 1976b; Gill & Wolf, 1975). These correlative studies showed that territorial behavior of nectarivorous birds was responsive to changes in territory quality, and emphasized the possibilities for a finer understanding of the dynamics of territorial defense.

Experimental manipulation of energy availability on feeding territories of Anna Hummingbirds *(Calypte anna)* showed that both intensity and methods of territorial defense were flexible with respect to territory quality; when the amount of energy available on a territory was reduced, owners shifted from energetically expensive chases to less expensive methods of defense (Ewald & Carpenter, 1978). However, defense occurred even when no rewards were available on the territory. This persistence suggests that prior quality of a territory influences the existence of territoriality.

In the present study I will focus my attention on two questions that arose from these studies of the past. First, can high prior quality of a territory result in defense of the territory even when it no longer provides a reward? Second, if conditions can be found where this influence does not exist, does the occurrence of territoriality agree with predictions derived from Brown's concept of resource defendability?

I investigated these questions using Anna Hummingbirds during the non-breeding season because at this time of year territorial costs and benefits can be indexed in calories (Ewald & Carpenter, 1978). Brown & Orians (1970) defined territoriality as a defended area that tends toward exclusive use by the resident with respect to rivals. I shall adhere to this definition during this study.

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Predictions from the defendability concept depend on how the birds measure costs and benefits of territorial behavior. If benefits and costs of both territorial and non-territorial strategies can be converted into units of energy, territoriality should occur when rate of net energy gain from being territorial is greater than rate of net energy gain from being non-territorial (Wolf, 1978).

However, gaining energy through territorial ownership might be preferable to gaining the same amount of energy without owning a territory; territorial ownership could provide more reliable access to energy over a long period of time (Brown & Orians, 1970), or non-territorial foragers might have increased risks of injury or death. If territoriality were the preferred method of gaining energy, it should occur when the energy gained on the territory is greater than the energetic cost of territoriality.

Unfortunately, the actual energetic cost of territoriality is somewhat enigmatic. For example, if a territory provides a small proportion of an owner's requirements, but the owner is capable of fulfilling the remainder in a small amount of time by foraging off of the territory, the owner would probably spend a large proportion of the day sitting. If sitting on the territory were no more costly than sitting off of the territory, these sitting costs should not be included in territorial costs. In fact, by this reasoning, the only costs which are clearly territorial costs are those in excess of an individual's metabolic rate while sitting. In this case

$$T = S - Mt \qquad \text{eq 1}$$

T is territorial cost in excess of sitting costs. S is total energy spent on and in transit to and from the territory. M is daytime metabolic rate while sitting. t is time on territory.

If sitting on the territory is costlier than sitting off the territory, or if time spent on the territory reduces an individual's total net gain, then at least part of the quantity Mt should be included in territorial costs. The maximum estimate of territorial costs includes all energy spent on and in transit to and from the territory, Thus, T is the minimum estimate and S is the maximum estimate of territorial costs. The actual costs probably lie somewhere in between. Consequently, the predicted threshold at which territorial gains equal costs will be a range of territorial rewards. The maximum value of this range will correspond to a territorial cost of S, the minimum value corresponds to a cost of T.

If territories are defended only when rate of net energy gain on the territory is greater than rate of net energy gain off the territory, a different threshold is predicted. The rate of net energy gain on the territory (N) can be calculated from the following equation:

$$N = \frac{E - T}{t - t_s} \qquad \text{eq 2}$$

E is the energy gained from the territory. t_s is time spent sitting on the territory. Rate of net energy gain from feeding at undefended resources is calculated analogously. Rates of net energy gain could also be calculated by using the relation $(E - S)/t$ and its analog for non-territorial individuals. The predicted thresholds are identical for these two methods if one assumes that both territorial and non-territorial animals expend energy at the same rate when they are not in foraging or territorial flight. However, the latter method is often intractable in the field. It requires that a non-territorial individual be followed continuously throughout a period of time long enough to obtain a realistic estimate of the proportion of total time spent sitting.

Influence from prior quality of the territory

Before evaluating the validity of these thresholds experimentally, it is essential to determine if past quality of the territory influences an owner's decision to defend the territory. It would also be useful to know how much of the past influences this decision.

I conducted the following experiment to test for these effects. Feeders providing .6M sucrose solution at an unlimited rate were presented for various lengths of time and then replaced by identical "dummy" feeders containing only water. The water feeders were observed at 2 h intervals for 10 min or until a territorial act occurred (whichever came first). When no territorial behavior occurred during two successive 10 min periods of observation, the interval between presentation of the dummy feeder and the last defense of the dummy feeder was calculated. The length of time that dummy feeders were defended is strongly correlated with the length of time unlimited sucrose feeders were owned (Spearman $r = .83$, $P \ll .01$, Figure 1).

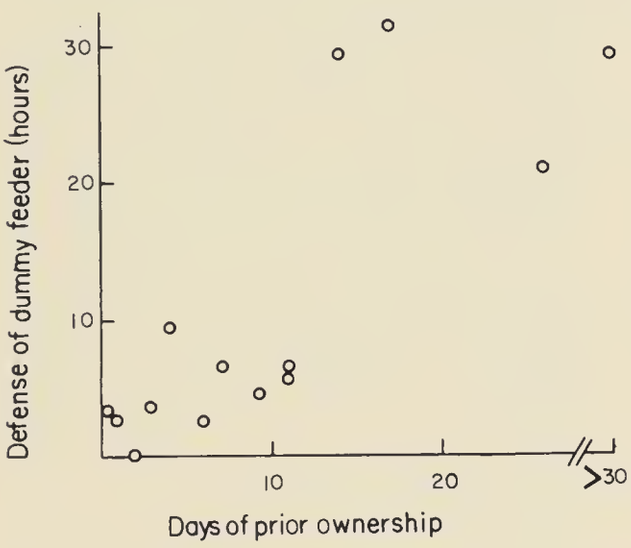

FIGURE 1. Number of daylight hours owners defended feeders containing water as a function of the number of days unlimited sucrose feeders were previously available on the territory.

An animal's ability to assimilate environmental information is of central importance to models of behavior. The data in Figure 1 suggest that territorial behavior in these hummingbirds is influenced by information acquired over many days. It is noteworthy that this time scale is similar to the lifespan of the flowers on which these hummingbirds feed.

Predictions of territorial thresholds

Estimates of territorial benefits and costs were obtained over a range of territory quality by the following procedure. Territorial rewards were reduced from an unlimited amount to zero by feeders with adjustable flow rates. One full day of observation was obtained at each level of energy availability except for the zero reward level which was based on a half-day of observation. Energy ingested by owners and intruders was deduced from the timing and sequence of visitations. I assumed a digestive assimilation efficiency of .98 (HAINSWORTH, 1974). Energy expenditures were estimated from time expenditures by methods described in EWALD & CARPENTER (1978).

Figure 2a shows when territorial gains equal territorial costs for maximal and minimal estimates of territorial costs. If territorial costs include all energy spent on the territory and in transit to and from the territory (i.e. costs = S), territoriality should occur only when

energy availability on the territory is .65× an owner's daily expenditures (Figure 2a, threshold B). If territorial costs include only the increased energy spent above sitting metabolism (territorial costs = T in accordance with eq 1), territoriality should occur when energy availability on the territory is .05× an owner's daily expenditures (Figure 2a, threshold A). These thresholds represent maximum and minimum thresholds predicted under the assumption that territoriality occurs when energy gained from the territory is greater than energetic costs of territoriality. By this assumption the actual threshold could occur anywhere between thresholds A and B.

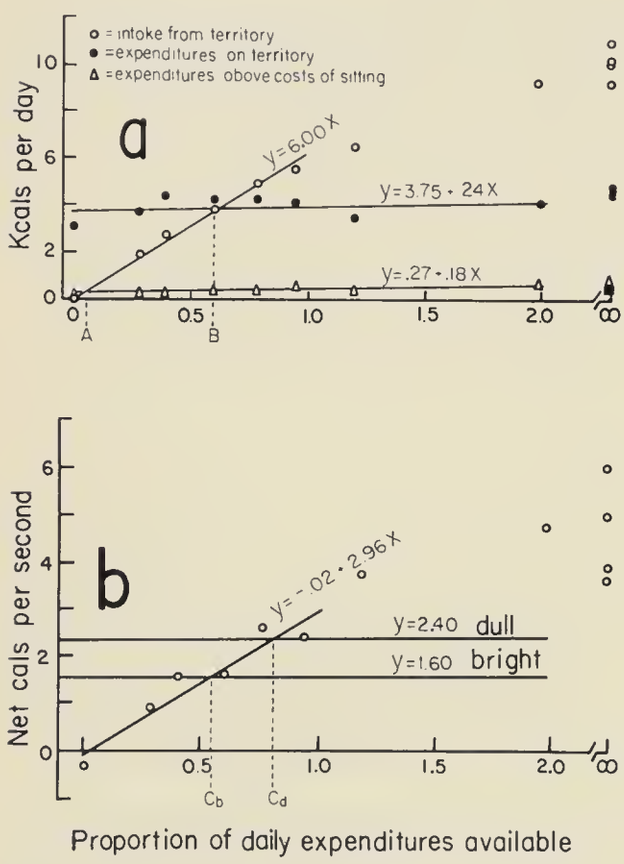

FIGURE 2.
Predicted thresholds of territoriality. Regressions for energy intake and rate of net energy gain on the territory were fitted to points below 1.0× an owner's daily expenditures because these variables should begin to plateau slightly above this level of energy availability. (a) Predicted thresholds assuming territoriality occurs only when energy gained on the territory is greater than territorial costs. Closed circles represent the maximum estimate of territorial costs (i.e. S). Triangles represent minimum estimates of territorial costs (i.e. T). Energy intake data (open circles) were regressed through the origin (STEELE & TORRIE, 1960) because the origin is a data point measured without error. (b) Predicted thresholds assuming territoriality occurs only when rate of net energy gain on the territory is greater than rate of net gain from intruding. Lower and upper horizontal lines represent rate of net energy gain by bright and dull intruders respectively on territories containing unlimited feeders.

If territoriality occurs only when the rate of net energy gain on the territory is greater than rate of net energy gain off the territory, a different threshold is expected. Net energy gain on the territory was estimated from the costs and benefits described above, using eq 2. The rate of net energy gain off the territory was obtained from the following experimental setup.

I maintained approximately 15 feeders at distances of 50 to 150 m from the site at which the actual threshold of territoriality was measured. Each feeder was defended by a single male, and flowers were extremely scarce in the area surrounding the study site. Thus, if a feeder with an adjustable flow rate were placed anywhere else in the study area, a hummingbird "contemplating" ownership of this feeder would have only one feasible alternative: to gain all its energy by intruding on the territories containing unlimited feeders.

The rate of net energy gain from this alternative was quantified by making the following measurements. Seconds of feeding and time spent per intrusion (sitting, hovering and linear flight to and from the territory) was measured for 251 intrusions. Time measure-

ments were converted into energetic units and the rate of net energy gain from intruding was derived by a direct analog of eq 2.

ROHWER et al. (in press) suggest that plumage coloration may influence an intruder's success at gaining access to defended resources. Anna Hummingbirds are highly variable in the amount of red feathering on their throat and forehead. To determine if birds with less red feathering were more successful at intruding, the amount of red feathering was estimated relative to the maximum amount for 211 intrusions. Birds were grouped into two classes: "dull" birds possessed less than 50% of the maximum amount of red feathering; "bright" birds possessed greater than 50% of the maximum amount. Dull intruders could obtain 6.5 kcals (an amount approximately equal to their 24 h energy requirements; EWALD & CARPENTER, 1978) in .93 h of intrusion time. Bright intruders required 1.52 h to obtain the same amount. For dull birds the rate of net energy gain on the territory equals rate of net gain from intruding, when the territory provides .82× an owner's daily energy expenditures (threshold C_d in Figure 2b). For bright birds this threshold occurs at .55 (threshold C_b in Figure 2b). These energy expenditures were based on weights of 4.86 g for bright birds (mean weight of 15 birds) and 4.87 g for dull birds (mean weight of 6 birds).

It is important to note that the predictions described above are based on data from territories that had previously contained richer food sources. As a consequence, I could obtain estimates of territorial costs even when the territory provided no rewards. A possible flaw in this approach is that cost estimates might be too high. The reality of this flaw could be tested by measuring costs on territories that did not previously contain richer food sources, and comparing them to the regressions in Figure 2a. If a discrepancy existed, a correction could be applied to the regressions.

Determination of the actual territorial threshold

An earlier section of this study showed that high prior quality of a territory can influence an owner's decision to defend the territory. I eliminated this influence during measurements of the actual territorial threshold by placing feeders with adjustable flow rates on areas which had not previously contained "nectar".

To obtain the acutal threshold the feeders were set at a specific rate and observed after a minimum of 6 h of exposure to the hummingbird population. If an act of defense occurred in a 1.5 h observation period the animal was assumed to be territorial. In one case the observation period was lengthened because a bird was present at the feeder for most of the observation period, but no intrusions occurred. When an intrusion finally occurred, it elicited a defensive response from the owner. This owner was assumed to be territorial.

TABLE 1: Presence and absence of territoriality at various levels of energy availability.
P= the proportion of an owner's 24 h energy expenditure available from the feeder per day.
T= the presence or absence of territoriality.
b = territoriality present, feeder owned by a "bright" bird.
d = territoriality present, feeder owned by a "dull" bird.
– = territoriality absent.

P	0.00	0.01	0.02	0.02	0.07	0.11	0.11	0.13	0.14	0.15	0.16	0.17	0.18	0.54	∞	∞
T	–	–	–	–	–	–	–	–	b	b	d	d	b	b	d	b

Total energy expenditures over each 24 h period were estimated from the following regression which was obtained from the data base of Ewald & Carpenter (1978):

$$E = 2.256 - 0.041\ T_a \qquad \text{eq 3}$$

E is kcals spent/g/day. T_a is mean ambient temperature over the 24 h period. ($r = .95$, $P \ll .01$)

Table 1 shows that feeders providing .13× an owner's daily expenditure or less were never defended. Feeders providing more than this value were always defended. This threshold is well below C_b and C_d (Figure 2b). Furthermore, dull birds had approximately the same threshold as bright birds (Table 1). The actual threshold is therefore inconsistent with the idea that owners are defending territories only when rate of net energy gain from the territory is greater than rate of net gain from intruding (Figure 2b shows that dull birds should have a far higher threshold). A greater risk of injury associated with intruding, or a greater long term net energy gain associated with owning a resource, could outweigh the increased rate of net energy gain from intruding.

The actual threshold lies between thresholds A and B but is closer to threshold A. This result is consistent with the idea that territoriality occurs when energy gained from the territory is greater than territorial costs. It also suggests that territorial costs include only a small portion of total energy spent sitting on the territory.

The results of this study may be applicable to a limited range of natural conditions; individuals acquired "nectar" from spatially concentrated sources either by owning a territory or by intruding on territories. In environments where undefended resources are available, risk of attack and injury to non-territorial individuals should be less. In such an environment a territorial threshold occurring when rates of net energy gain on and off the territory are equal is still a likely possibility.

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Resource Limitation, Foraging Strategies, and Community Structure in Hawaiian Honeycreepers

F. Lynn Carpenter and R. E. MacMillen

The Hawaiian honeycreepers, endemic family Drepanididae, are renowned for their remarkable adaptive radiation and for the recently high incidence of extinction of species. Thus, it is of great interest to understand the ecological factors that regulate the population densities and community structure of extant species.

Berger (1972) has noted that 40 percent of drepanidid species have gone extinct, most around the turn of the century. Coincident with these extinctions were the introductions of domestic grazing and browsing animals and the clearing of much forest for agriculture. Because many species were known to have specific habitat preferences, it seems simple to explain extinctions and present-day low population densities of certain extant species by habitat destruction.

However, Warner (1968) disagreed that habitat destruction has been the primary cause of population declines. He noted that early authors described undisturbed lowland forests becoming devoid of their bird populations (Henshaw, 1902) or species going extinct whose habitat had suffered no disturbance, or species going extinct on Oahu but not on other islands where habitat was even more restricted. Munro (1944) recorded the disappearance of the native birds on Lanai over the short duration of 10 years even though their habitats were essentially intact on that island at the time. He believed that introduced diseases were to blame, and Warner (1968) supported this by demonstrating the susceptibility of drepanidids to bird malaria and bird pox and noting that the upper elevational limit of the mosquito vector coincides with the present-day lower elevational distribution of extant drepanidid (~ 600 m).

Table 1: Comparison of nectar-eating birds on Hawaii

Family and species	body length [1] (cm)	bill length [2] (cm)	nectar specialized?	populational status
Meliphagidae				
Moho nobilis	31.7	2.7	yes	extinct
Drepanididae				
Drepanis pacifica	19.7	4.3	yes	extinct
Vestiaria coccinea	14.6	2.7	yes	6% of avifauna [3]
Himatione sanguinea	13.3	1.7	yes, less than *Vestiaria*	34% of avifauna [3]
Loxops virens	11.4	1.35	no	13% of avifauna [3]

[1] from Peterson (1961).
[2] Our measurements on specimens in the Bishop Museum from the island of Hawaii. Sexes averaged.
[3] from Conant (1975).

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Nevertheless, the disease hypothesis does not explain why, within the high elevation refuges from disease vectors, it has been populations of the larger-bodied, morphologically specialized species that have gone extinct or drastically declined (Table 1). This pattern suggests that some interaction between food and habitat availability may have contributed to the extinctions, and may continue to be of importance in the population and community ecology of extant drepanidids in their high elevation refuges. As with any group of coexisting species, it is difficult to unravel important limiting factors on populations, especially if experimental techniques such as population removal or resource manipulation are not feasible. However, it is relatively simple to assess the availability of flower nectar as a resource to nectar-eating species and to determine if the supply just balances the needs of the populations or is present in excess. With this in mind, we set out to investigate the nectar resource for the three commonest species of nectar-eating drepanidids on the island of Hawaii, the Amakihi *(Loxops virens),* the Apapane *(Himatione sanguinea),* and the Iiwi *(Vestiaria coccinea),* and their behavioral responses to each other in relation to the nectar resource.

We studied the community between 1230 and 1850 m on the slopes of Mauna Loa for three consecutive summers beginning in 1973, and found that in two of these years, nectar was superabundant relative to the requirements of the birds. Bird densities remained approximately similar over the three years, but flower densities of their primary summer nectar resource, *Metrosideros collina,* varied. In 1973 and 1975 from 2 to 5 times more nectar was available than in 1974 (CARPENTER,1978; CARPENTER & MACMILLEN, in review, a). By the end of the foraging day from 3.5 to 5.6 cals on the average remained unexploited in the flowers. In contrast in the poor bloom year 1974, the average value for unexploited nectar was 0.8 cal/flower. We calculated that the three species range in requiring from 0.5 to 0.9 cal/flower on the average to pay for the cost of a flower visit alone, whereas 0.8 to 1.5 cal/flower are required to balance their 24 h energy budget. *Loxops virens* required the least, so that nectar availability was barely enough to support this species, but it was apparent that in 1974 nectar was in short supply to the two nectar specialists and was being fully exploited. In contrast, during the other years nectar was so superabundant that only a fraction of the nectar produced was being exploited. Therefore, food is at times a limiting resource to these populations. Our summer studies were conducted after the completion of the winter-spring reproductive period of the birds, so nectar limitation at these times would affect populations by lowering individuals' chances of survival during the dry nonreproductive season. Did the avian behavior in nectar-scarce 1974 seem to reflect a stressful resource situation?

Nectar limitation means that interspecific competition for nectar occurs and selection should favor efficient strategies for nectar foraging or else diversification of diet. Competition was of the interference type, as seen also in hummingbirds. In the nectar-superabundant years, the three species coexisted peacefully in flowering *Metrosideros* trees, but in 1974 aggression erupted (CARPENTER, 1978). The largest, most nectar-specialized species, *Vestiaria,* became intra- and interspecifically territorial, monopolizing the richest flower patches (CARPENTER & MACMILLEN, 1976a, 1976b). The intermediate-sized *Himatione,* which is also intermediate in degree of specialization for nectar, had large foraging areas and defended a small volume around their immediate position as they moved through foraging. Defense was primarily against *L. virens* but

some intraspecific defense occurred also. Finally, the totally subordinate *L. virens* was effectively excluded from the flower resource by the two more dominant, larger, specialists (CARPENTER & MACMILLEN, in review, a). *L. virens* is a dietary generalist, and although it persistently attempted to obtain nectar from flowering *Metrosideros,* it was quite unsuccessful and spent most of its time gleaning for insects. Thus, when nectar was scarce, the resource was partitioned by species-specific monopolization of different resource densities: the largest specialist occupied the richest patches, the intermediate species occupied moderate to low flower densities, and the small generalist occupied areas with few or nor flowers. Density partitioning has been documented in nectar-feeding bees (JOHNSON & HUBBELL, 1975) and in a system of territorial and traplining hummingbirds (FEINSINGER, 1976). The mechanism for density partitioning in all these systems is aggression, and in our system dominance was correlated with both body size and degree of morphological specialization on nectar. Interestingly, the writings of PERKINS (1903, 1913) at the turn of the century, when the larger nectar-specialized species of *Moho* (Meliphagidae) and *Drepanis* still existed on Hawaii, contain observations that suggest that *Moho,* the largest, was aggressively dominant at times to *Drepanis,* which in turn was dominant to the other smaller nectar feeders. He noted *Vestiaria*'s dominance at times to the smaller honeycreepers, but also described examples of peaceful coexistence between several of these species. Perhaps the apparent conflict in these observations stemmed from his making observations during times both of nectar abundance and of nectar scarcity just as we did.

BALDWIN's (1953) thorough study revealed that *Vestiaria* and *Himatione* follow the bloom up and down the mountain slopes through the year; *L. virens* is more sedentary and its movements are independent of the bloom. CARPENTER & MACMILLEN's (in review, a) correlation analysis of BALDWIN's data showed that *Vestiaria* tracks the bloom closely whereas *Himatione* tends to lag a few weeks behind. These results were predictable on the basis of morphological specialization for nectar: the most nectar-specialized species, based on bill morphology *(Vestiaria),* should track the bloom best, and the most morphologically generalized species *(L. virens)* could be expected to move independently of the flower resource. *Himatione* apparently can exist for a while on a relatively high ratio of insects:nectar before it moves on following the bloom.

Fluctuation of resource availability from year to year in our study was correlated not only with aggressiveness but also with differences in daily sedentariness and other aspects of foraging behavior. In the nectar-limited year, all three species were largely sedentary during the day and we were able to resight or renet 14 – 37% of our banded individuals, depending on species. In contrast, in 1973 we renetted no individuals. In 1975, observed *Vestiaria* individuals vacated their foraging areas for longer periods than in 1974. Thus, in nectar-abundant years *Vestiaria* and *Himatione* were certainly more mobile than in 1974. *Himatione* roost in a common roost area at an intermediate elevation, and our data (CARPENTER & MACMILLEN, in review, b) suggest that they leave their roost at dawn, fly some distance from the roost to their initial foraging areas 3 – 9 km away, and then work their way foraging slowly back toward the roost all day. At dusk they form loose flocks and fly the rest of the way to the roost. This kind of mobile foraging strategy occurred only at times when the bloom was good and fairly homogeneous across the forest; it did not occur in the nectar-sparse year when the bloom was not only poor but also very patchy.

The increased sedentariness which correlated with nectar scarcity means that fewer unexploited flowers were available to each individual forager. Thus, each individual should manage that limited resource in a more efficient way than when foraging in its mobile manner during nectar-abundant years. We looked for sequential foraging by individuals on their areas such that flower revisitations would be spaced temporally to allow nectar replenishment in their diurnally secreting (CARPENTER, 1976) flowers. We could not study this in *Himatione* because it was difficult to dependably sight banded individuals and keep them in view on their large home ranges for very long. But two territorial *Vestiaria* evenly spaced revisits to specific portions of their territories, thereby increasing foraging efficiency (CARPENTER & MACMILLEN, in review, b). Such time-patterning has also been described in African sunbirds (GILL & WOLF, 1977). Interestingly, across the island of Hawaii on the slopes of Mauna Kea where *L. virens* occurs in absence of the two dominant nectar specialists, it defended feeding territories intraspecifically and time-patterned flower revisits just as did *Vestiaria* (KAMIL, 1975). This study was done summer 1975 and it was unknown whether the nectar source *(Sophora chrysophylla)* was sparse or abundant relative to the birds' requirements in this area.

Nectar scarcity thus leads to increased aggressiveness, territoriality, decreased mobility, density partitioning of the resource, competitive exclusion of a generalist from the resource, and increased foraging efficiency. It seems abundantly clear that resource limitation and competition, therefore, are important factors affecting the populations of these species of honeycreepers within their present-day distributions. If competition was important at least sporadically in the past, then a reason for the apparently higher susceptibility of the large nectar-eating species to extinction or general population decline can be surmised. Table 1 compares the five nectar-eaters that coexisted on Hawaii. The two smaller nectar-eaters require less total energy per individual than do the larger specialists, and in times of nectar scarcity are less aggressive and can get along to some extent on alternative food sources. Therefore, although we believe MUNRO (1944) and WARNER (1968) were probably correct in attributing the shrinkage of drepanidid distributions to higher elevations to avian disease, within those smaller islands of habitat the large species would have needed more food resource to maintain population densities. A year or two of poor bloom could have reduced their numbers to inviable levels, whereas the smaller more generalized species could still survive. So we believe that a combination of disease, habitat reduction, and competition for a limited, specialized food likely explains the selective reduction of populations of the large species while the small species have continued quite successfully. Since clearing of vast tracts of *Metrosideros* forest continues on the island of Hawaii today, we shall not be surprised if the next nectar-eating drepanidid to go extinct will be *Vestiaria coccinea,* as it already has on Oahu and Molokai.

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Resource Gradients and Community Organization of Nectarivorous Birds

Larry L. Wolf and Frank B. Gill

Introduction

Specialized nectar feeding birds acquire most of their energy resources from floral nectar, the characteristics of which determine the organization of assemblages of these species (Feinsinger, 1976; Wolf et al., 1976). The availability of insects as a nutrient source and the avoidance of predation seem to be secondary, indirect influences on community structure. We often can estimate the total nectar resources available to nectarivores (Carpenter, 1976a; Gill & Wolf, 1977) as well as define niche relationships in terms of potential and realized foraging efficiencies (Wolf et al., 1976; Gill & Wolf, 1979a). Consequently, these birds are important sources of information on community organization.

The communities of nectarivores studied to date are dynamic assemblages, reflecting changes in local climatic conditions and the temporary nature of plant flowering. Seasonal variations in the availability of floral nectar include: (1) total flowers and amount of nectar per flower; (2) species composition of simultaneously flowering plants; and (3) asynchronous blooming or productivity of plant species competing for the same avian pollinators (Stiles, 1975). Flowering can and does occur throughout longer periods of the year in less seasonal areas; but even sites in the humid lowland tropics of Central America have few flowers at certain times of the year. Within the genus *Heliconia* in the humid lowland forests of northeastern Costa Rica there are periods during which many species bloom, but synchronous forms are segregated by habitat and also by morphological and physiological characteristics that attract different hummingbirds (Stiles, 1975). In East Africa plant species often bloom asynchronously and also are geographically separated so that the nectarivorous sunbirds must move from one bloom to another, changing locality as well as plant species (pers. obs.)

We must consider both the variations in foraging efficiency of particular bird species at particular flowers, and the temporal dynamics of arrivals and departures by different species at a locality to understand the community structure of nectarivorous birds (Culver, 1970; Simberloff, 1969; 1974). Communities that are dynamic on a seasonal and perhaps even daily basis should be good places to search for what Diamond (1975) has called assembly rules of communities. Just how are species added to or subtracted from existing assemblages? If the critical niche characteristics defining these assembly rules vary, are the rules the same for periods of addition and the periods of subtraction? If the system is dynamic, is it ever in equilibrium or is there always a time lag between the changing resource levels and the response of the community? Time lags would have the tendency to produce marked instability of the community structure in a manner similar to the effect of time lags in single species population growth models (e.g., May, 1976).

One approach to assembly rules is to define the apparent "roles" of individuals in nectarivore communities and to see which of these roles are filled in communities of

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varying complexity (Feinsinger & Colwell, 1978). We have attempted, in this paper, to define the positions that individuals can occupy along the nectar-based resource gradient and to use this information to predict which positions along the gradient are likely to be available in particular communities. To the extent that these positions can be categorized they approximate to part of the definition of roles outlined by Feinsinger & Colwell (1978).

Resource Gradients

We assume that the fitness of a nectarivore is associated with its foraging efficiency, defined as the rate of net energy gain (Gill & Wolf, 1977; Gill, 1978; Pyke, 1978; Hainsworth & Wolf, 1979). The interactions of bird and flower morphology, the availability of energy, and the costs of obtaining that energy affect an individual's foraging efficiency and can be ordered as bird-defined gradients in resource quality (Gill, & Wolf, 1975a, 1979b). This means that the same resource base, even across multiple plant species, can be viewed as a single resource type within which quality differences are defined by both the birds and the flowers. The variables that are important in defining the quality gradient for an individual nectarivore are listed in Table 1.

Table 1: Variables affecting the foraging efficiency of nectar feeding birds

plant characteristics	bird characteristics
floral morphology	bill morphology
corolla length and shape	bill length and curvature
corolla diameter	bill width
location of nectary	tongue volume
floral physiology	body size
nectar production rate	metabolic costs
nectar volumes	dominance and feeding priorities
nectar molarity	wing disc loading
flora dispersion	competition
flowers per inflorescence	exploitative losses
flower density	interference costs

Bird species vary in their ability to obtain the nectar reward at a particular plant species (Gill & Wolf, 1975a; Wolf et al., 1972, 1976; Wolf & Wolf, 1976; Gill & Wolf, 1979b). The corolla length determines how far the bird must reach to obtain the nectar. The rate at which an individual can extract the nectar is a function of this distance, the available nectar volume and the tongue volume (Hainsworth, 1973; Schlamowitz et al., 1976; Hainsworth & Wolf, in prep.) The proportion of tongue volume filled decreases as distance to the nectar increases and as nectar volume decreases, both slowing the rate of exploitation. Curved corollas are often easier for curve-billed birds to probe than for straight-billed birds (Snow & Snow, 1972; Wolf et al., 1972).

Net benefits of foraging depend on the metabolic costs associated with foraging that must be subtracted from the gains. These costs depend on size (Calder & King, 1974; Brown et al., 1978), relative wing length (Epting & Casey, 1973), and foraging method

(i.e., proportion of time flying; WOLF et al., 1975). The costs of moving between flowers vary inversely with flower density and the influence of these costs on the total energy budget increases disproportionately with increasing body size (HAINSWORTH & WOLF, 1972).

The rate at which different-sized nectarivores obtain net benefits generally varies monotonically with position on the resource quality gradient (Fig. 1). If the quality gradient is defined in terms of flower density then rate of net gain is inversely related to body size because of the changing flying costs (Fig. 1a). If the quality gradient is defined in terms of nectar volumes or corolla lengths rate of net gain is proportional to bill length (Fig. 1b), which is often correlated with body size. These functions could be strongly curvilinear (WOLF et al., 1975) but the details of shape are not critical to the major point of this discussion.

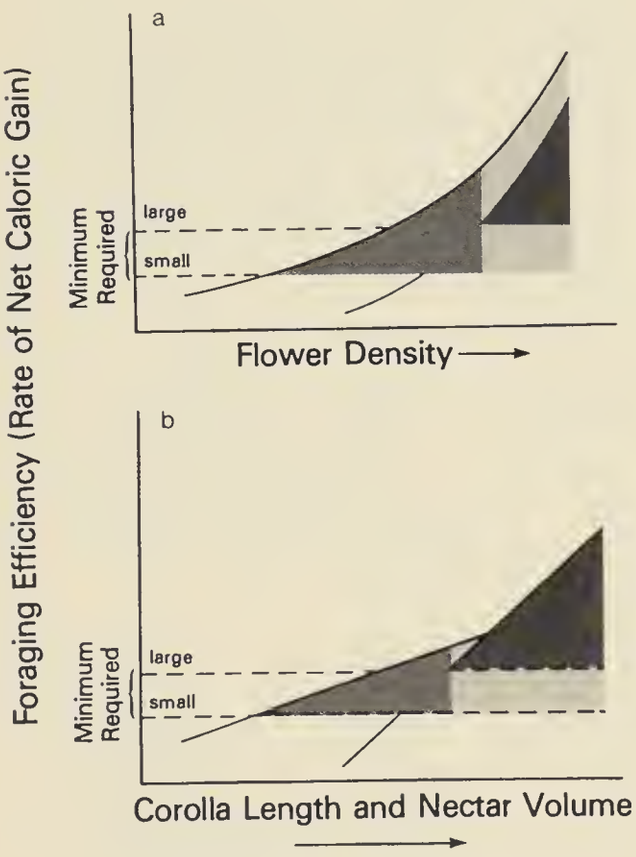

FIGURE 1. Coexistence of a large and a small nectarivore on a resource quality gradient. The minimum foraging efficiency required to maintain a balanced 24-hr energy budget is higher for the larger species because of its greater total daily energy costs. The intersections between the curves specifying achieved foraging efficiency at a particular point on the resource gradient and the minimum required value specify the lowest portion of the resource gradient occupiable by each species. The large species with its higher costs is restricted to the high end of the gradient shown here by the cross hatched triangular area. The small species is restricted by the larger species through aggressive dominance to the low end of the gradient not occupied by the large species, shown here as a solid dark triangle. Potentially the small species can occupy a larger area in the absence of the dominant, indicated here with light stippling.

When the resource gradient is defined in terms of flower density (upper) the small species has a higher foraging efficiency than the large species because of its lower flight costs. This advantage increases as the distance between flowers increases. When the resource gradient is defined in terms of increasing nectar volumes and corolla lengths (lower) the large species has a higher foraging efficiency at flowers with long corollas with high nectar, but not at flowers with short corollas and low nectar volumes.

Each species potentially can use those positions on the quality gradient where it can achieve a rate of net benefit sufficiently high to replace nonforaging costs over some specified time period, usually 24 hours. The intersection of the foraging efficiency curve and the minimum required foraging efficiency defines the lower limit of use on the quality gradient by each species or individual (Fig. 1). Each individual should preferentially exploit resources at the high end of the quality gradient to the degree these are available.

The potential positions of these birds on the resource quality gradient are analogous to one dimension of the fundamental niche functions of the theoretical community ecologist (Hutchinson, 1957). The realized niche, on the other hand, represents actual use along the same gradient, reflecting, especially in these systems, aggressive displacements and interference competition (Case & Gilpin, 1974; Gill, 1978; Wolf, 1978). Large nectarivores have the advantage in aggressive interactions (Wolf, 1970; Wolf & Gill, in prep.) and can usurp the best portions of the resource gardient. If we assume that an individual that is dominant must maintain at least a neutral 24-hour energy balance it will be able to usurp all portions of the gradient above that break-even point. This point defines the maximum possible foraging efficiency and the upper limit of the realized niche of the subordinate form in the presence of the dominant (Fig. 1).

Large body size assures priority access to the upper portions of the resource gradient, but at the same time reduces the range of usable resources compared to subordinates. The composition of a nectarivore community, therefore, depends on the spectrum and availability of resources. The narrow resource spectrum usable by the large dominant coupled with the natural variations in flower availability will make it unlikely that this form is a regular member of the community. Medium body size confers the advantages of some dominance and a broader range of usable resources. The resident, foundation species (Dayton, 1975) of tropical hummingbird communities is usually such a moderate-sized form – e.g., *Panterpe insignis* in the high mountains of Costa Rica (Wolf et al., 1976), *Amazilia saucerottei* at intermediate elevations of Costa Rica (Feinsinger, 1976) and *Sericotes holosericeus* in the Lesser Antilles (Lack, 1973). The absolute size of this foundation species will depend on characteristics of the resource gradient. The foundation species in north temperate hummingbird communities are slightly smaller than those reported from most tropical communities (Stiles, 1973; Gass et al., 1976; Kodric-Brown &Brown, 1978). Small subordinate species should consistently exploit the low end of the resource spectrum and opportunistically exploit overlapping portions of the resource gradient not fully used by more dominant forms.

The range of dispersion patterns, floral traits, and nectar characteristics increases with the diversity of food plants. Simultaneous combinations of these factors in natural communities increase the complexity and dimensionality of the resource gradient and, therefore, the number of nectarivore species that can be added to a community. In general, additional species will be ones specializing on portions of the resource spectrum not used by the dominant generalist or foundation species. These additional species include large forms with highly specialized bills such as the hermit hummingbirds *(Phaethornis* spp.), the Starthroats *(Heliomaster)*, and perhaps the Sabrewings *(Campylopterus* spp.). At the other extreme are very small species that can exist on what would be low efficiency flowers for the foundation species. These include such genera as *Microchera*, *Klais*, *Chlorostilbon*, and *Orthorhyncus* in the lowlands of the Neotropics. Some of these forms exist at the margins of the quality gradient for other species.

The extent that these peripheral forms will be present strongly depends on what limits the population sizes of the dominant generalist forms. These population sizes may be controlled outside of the particular season being investigated and not able to saturate the available quality resources. In this case some of the peripheral forms will be able to maintain a position or seasonally invade the community. Invasion is less likely if the dominant generalist can control most or all of the available resources.

Temporal Dynamics

Spatiotemporal variation in flower availability necessitates a continuum of possible migratory responses by nectar-feeding birds. North temperate hummingbirds regularly undertake major migrations (STILES, 1973; GRANT & GRANT, 1968) while some tropical lowland forms may not move more than a km or two throughout their life span (STILES & WOLF, 1979). Most neotropical hummingbird communities where floral nectar is available all year long include both resident and migrant species (SKUTCH, 1967; STILES, 1975; WOLF et al., 1976; FEINSINGER, 1976; CARPENTER, 1976b). Other nectarivores also may undertake major nomadic or migratory movements. These are well known for Australian honeyeaters (KEAST, 1968), Hawaiian honeycreepers (BALDWIN, 1953) and some sunbirds (SKEAD, 1967).

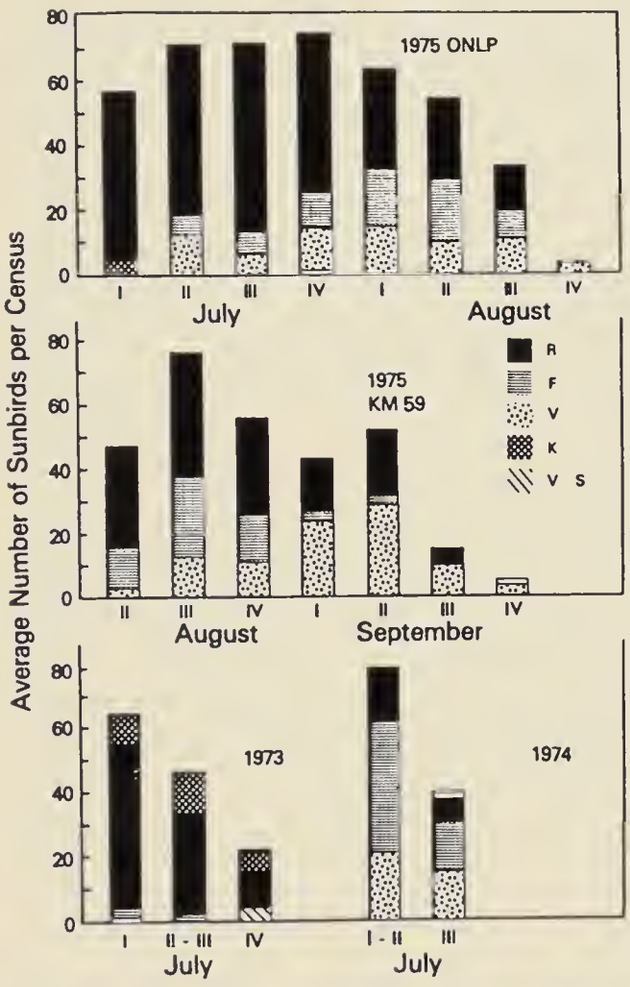

FIGURE 2. Absolute and relative abundances of several sunbird species at flowering patches of *Leonotis nepetifolia* in the Rift Valley of Kenya. The upper and middle figures are for patches that bloomed in sequence about1 km apart near Longonot. The bottom figure is for an area near Lake Naivasha about 25 km from Longonot and contrasts sunbird population structure in sequential years. The censures are grouped by weeks within each month.

Nectarivore communities then are composed of permanent residents and temporary residents. This places a major emphasis in understanding such communities on the importance of migration and on the probabilities that forms will arrive at a particular site in sufficient numbers to saturate the system. Local nectarivore communities are tied to other such communities by interactions that influence movements of the component species. Therefore temporal differences in community structure may be determined partly by conditions elsewhere. In July to September 1975, two large patches of *Leonotis nepetifolia*, a weedy mint, bloomed sequentially in areas about 1 km apart in the Rift Valley about 55 km north of Nairobi, Kenya. Each patch was visible from the other. In the first bloom dominant sunbird species, primarily Golden-winged Sunbirds *(Nectarinia reichenowi)*,

were numerically most important (Fig. 2). There was very little movement of marked birds from the first to the second bloom. At the second bloom subordinate forms, including Malachite and Variable Sunbirds *(N. famosa* and *N. venusta)*, were numerically predominant. We hypothesized that the Golden-winged Sunbirds had moved to higher elevations where another species of *Leonotis, L. mollissima,* was coming into bloom. Similar variation in composition of a sunbird assemblage can be seen in data from a single location in two consecutive years (Fig. 2). In the first year, dominant forms, both Golden-winged and Bronzy *(N. kilimensis)* Sunbirds, were numerically predominant, while in 1974 these dominant forms were mostly absent and subordinate species predominated.

Arrival rates and population sizes of nectarivores are more stochastic than typical community models usually incorporate (except, e.g., MacArthur & Wilson, 1967; Horn, 1975; Caswell, 1976). The stochasticity in the organization of nectarivore communities is probably not qualitatively different from many other types of communities, but it is perhaps more obvious. The degree to which the stochastic influences are important will vary with the movement patterns of the component species. Our search for assembly rules for the nectarivore communities must incorporate these stochastic processes along with responses to competition for the available nectar resources (Wiens, 1977).

Another aspect of this stochasticity is the size of populations relative so the resource availability (Wiens, 1974). Nectarivores generally are not continuous breeders so there always will be a time lag between good conditions and increases in population size. Depending on the degree to which migratory responses are possible the nectarivores available to join a community may not vary directly with the resource levels of that community. On a shorter time scale it is possible that periods of good bloom locally are also periods of good bloom over a broader area. This means that some exceptionally dense blooms may have few birds exploiting them. In August-September, 1975, in the Rift Valley, *Leonotis nepetifolia* was in exceptionally intense bloom. The *Leonotis* at one location was exploited almost entirely by few individuals of subordinate species of sunbirds (e.g., *N. famosa* and *N. venusta*), and facultative nectar feeders such as white-eyes *(Zosterops)* and weaverbirds *(Ploceus)* that normally are not seen at these flowers (Gill & Wolf, unpubl.). Nectar volumes per flower reached exceptionally high levels (>20 μl). The details of heavily used versus lightly used flowering areas may differ considerably, both in species structure and the overt character of the aggressive social organization (Wolf, 1978).

The East African bird-flower systems perhaps are more amenable to analyses of local community structure than tropical hummingbird communities since many of them involve a variety of bird species exploiting flowers of a single plant species. The same set of sunbird species is found at flowering *Leonotis* spp., *Aloe* spp., and *Loranthus* spp. (Gill & Wolf, 1975a, b, 1977; Wolf & Wolf, 1976; Moreau, 1966; Cheke, 1971), but blooms of each of these plant species often are temporally and spatially distinct. Consequently, when one bloom is finished the individuals within a community soon will be required to reassociate in a different context.

These single plant species systems in East Africa are similar to islands with no initial colonists. However, the resources are present for a relatively short time and change continually. Each flower bloom can be colonized by available individuals and then may go

through some phases of community development outlined by Wilson (1969), i.e., non-interactive, interactive, and assortative. The short time scale involved in these blooms precludes evolutionary changes, but each bloom can at least progress through the non-interactive and interactive phases if colonization does not lag too far behind the changing resource levels. Whether the nectarivore community ever reaches the assortative stage depends on the length of the bloom and the arrival probabilities of each species. The potential for invasion is a function of the availability of unexploited resources which itself is a continually changing variable.

At a sunbird assemblage associated with *Aloe kedongensis* near Gilgil, Kenya, in 1975 (Wolf & Gill, in prep.), the abundance of flowers essentially followed a normal curve with a strong peak midway through the nine week blooming period. The temporal pattern of bird biomass was very similar. However, the resource content of the bloom increased faster than the ability of the dominant species of sunbirds, including new arrivals, to use it. Resource levels available to subordinates, measured as nectar per average flower and total number of available flowers, then increased as the bloom progressed to its peak. The reverse trend occurred as the bloom intensity subsequently declined. The percentage of subordinates in the assemblage increased to the peak of the bloom and then declined in the mirror image of the increase, paralleling the progression of flower density and average nectar volumes per flower. There was no noticeable time lag in response of the subordinates during the bloom's increase or decrease, suggesting a dynamic equilibrium. In this case the equilibrium was maintained by a continually available pool of subordinate immigrants that could exploit nectar not used as a result of the low level of immigration of dominant forms.

The relative importance of stochastic events in the final organization of an equilibrium community may produce multiple community types within the same community system through time. In years with a high population of dominants relative to nectar availability the low availability of nectar would enhance aggressive interactions by the dominants, thus restricting the entry of subordinate forms into the assemblage. Perhaps these could be viewed as the multiple domains of attraction of Gilpin & Case (1976). To the degree that the short term availability reduces the probabilities of colonization many flower systems are likely to show different levels of approach to the phase of strong competitive interactions.

Most of the sunbird-flower systems are probably at or near an equilibrium of resource availability and bird population sizes. These equilibrium systems show relatively rapid shifts in organization as the resources change. As the locations of the flowering and the intensity of the flowering become more predictable, so does the organization at the equilibrium condition. When the systems are as unpredictable in time and space as they appear to be in East Africa, with the very local weather-influenced patterns of blooming (plus human influence in the form of habitat disruption), it is more likely that there will be major differences in community organization between successive blooms at the same locality.

Hummingbird and sunbird communities qualitatively are organized approximately the same. The degree to which the system can be monopolized by moderate sized or large individuals will determine how many subordinate forms can be inserted. In the single flower systems of East Africa there are fewer specializations that can be added compared to

the more diverse flower systems of neotropical hummingbird communities; it is unlikely that an extreme specialist of large size will evolve as the range of flower types that must be exploited throughout the year is relatively broad. The same organizational rules should also hold for the Hawaiian honeycreepers (Drepanididae) and the Australian honeyeaters (Meliphagidae). However, the degree to which each of these systems is nectar-limited may vary (Carpenter, 1978).

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SYMPOSIUM ON
ECOLOGY AND SYSTEMATICS OF THE GENUS PASSER

10. VI. 1978

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Flock Organization and Feeding Budgets in a Field Population of House Sparrows *(Passer domesticus)*

C. J. Barnard

Introduction

Recent theoretical and empirical investigations into the organization of feeding behavior in flock-feeding birds have shown that the size and composition of the flock may play an important role in deciding the amount of time a bird invests in each kind of behavior performed in a feeding bout (Pulliam, 1973, 1975; Pulliam et al., 1974; Parker & Stuart, 1976; Caraco, MSS a and b). The amount of time a bird invests in performing each behavior or the frequency with which each behavior is performed can be described as the bird's feeding budget, and a bird should seek to maximise the benefit/cost ratio of its feeding budget in accordance with the selective pressures in the environment (Caraco, MS a).

If this is the case we might except the organization of flocking behavior and its role in determining feeding budgets to vary between habitats that differ in the selective pressures they impose. In this paper I present a summary of some field observations I made on overwintering populations of House Sparrows at a farm just outside Oxford, England, in 1976—1977 and 1977—1978. The observations were designed to test the hypothesis that flock organization and feeding budgets varied between two habitats that contrasted in terms of the risk of predation to feeding birds.

The cattleshed and open field habitats

The area of the farm in which the sparrows were regularly active could be divided into two distinct habitats: cattlesheds and open fields. Both habitats provided food in the form of barley seed, although in the cattlesheds seeds were concealed in bedding straw. At the time of year when I made observations in the open fields (October/November), seed density was much higher than during the mid-winter period owing to harvest debris and the new-sown winter crop, and densities were comparable with those in the cattlesheds. However, although the two habitats were broadly similar in terms of food availability, they differed markedly in the risk of predation they imposed on feeding birds.

In the cattlesheds the only predators were feral cats *(Felis catus)*, of which the farm provided a population of six. However, the cats seldom ventured into the cattlesheds because there was little cover for concealment and they were constantly disturbed by the movements of cattle. They therefore presented little threat to birds feeding actually within the sheds. Apart from two brief visits by a male Kestrel *(Falco tinnunculus)*, I did not see any aerial predators in or around the farm buildings (during approximately 900 hours of field observation), and the only other environmental factors that could loosely be described as "predators" were cattle, the movements of which presumably constituted some sort of threat from trampling, and the farm staff, whose activities appeared to create the greatest disturbance to feeding birds.

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In the surrounding open fields, however, birds were completely exposed to attacks by aerial predators. Two pairs of Kestrels and an adult female and juvenile Sparrowhawk *(Accipiter nisus)* were resident near the farm and regularly patrolled the hedges and fields. Even though the number of attacks I observed was low (Barnard, in press), one or more raptors was present in the vicinity of the fields for a large part of the day. Two of the feral cats also patrolled along the hedges and frequently concealed themselves in the foliage.

The organization of flocking in the two habitats

The difference between the habitats in the risk of predation to feeding birds was reflected in the way flocks were organised. In the cattlesheds, there was little tendency for birds to arrive at or depart from a feeding site in cohesive groups. Birds tended to arrive singly and there was a random distribution of intervals between arrival times of successively arriving birds. In the open fields birds tended to operate from cover (hawthorn hedge) and seldom fed more than 15—20 m away from a hedge. Intervals between arrivals were generally short and birds never moved independently between a

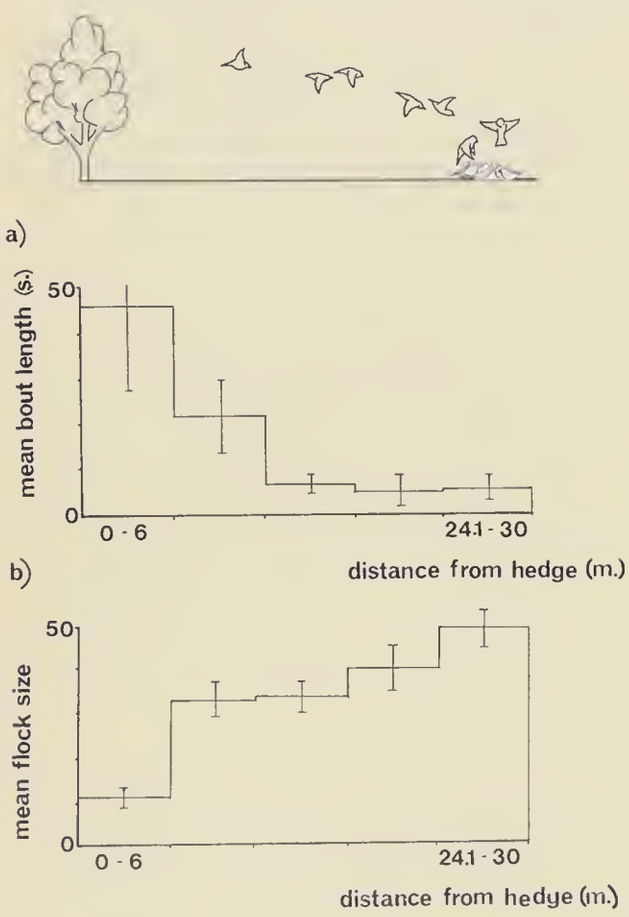

Figure 1. a) The change in the mean length of flock feeding bouts with distance from cover. n = 42 bouts. Bars represent standard errors. b) The change in the mean number of birds in a feeding flock with distance from cover. n = 38 feeding bouts.

feeding site in the field and cover; rather they always moved as a unified flock. The length of flock feeding bouts varied inversely with distance from cover but the size of feeding flocks showed a positive correlation with distance (Fig. 1). These observations suggests that birds were responding to the increased risk of predation when feeding away from cover. Furthermore, flocks in the cattlesheds frequently reached an equilibrium in size (Krebs, 1974) where the rate of arrival equalled the rate of departure. In the open fields flocks were never seen to reach an equilibrium size, because bouts

usually lasted only 7 to 10 seconds and also because birds were reluctant to behave independently of the flock.

The organization of feeding budgets

On average 94 % of the recorded behavior an individual performed during a feeding bout consisted of three mutually exclusive acts: pecking, hopping, and upright looking (hereafter referred to as "looking"). The remaining 6 % consisted mainly of fighting, but also included some head-cocking, which was occasionally performed independently of hopping. The time budget of the birds was therefore defined as being comprised of pecking, hopping, and looking, reflecting respectively energy intake, moving about the feeding site, and scanning the environment for predators. Looking was assumed to reflect vigilance for predators, rather than looking for food or conspecifics for example, because it characteristically occurred during disturbance or just prior to flight, and has been associated with vigilance for predators in other species (e.g., LAZARUS, 1972).

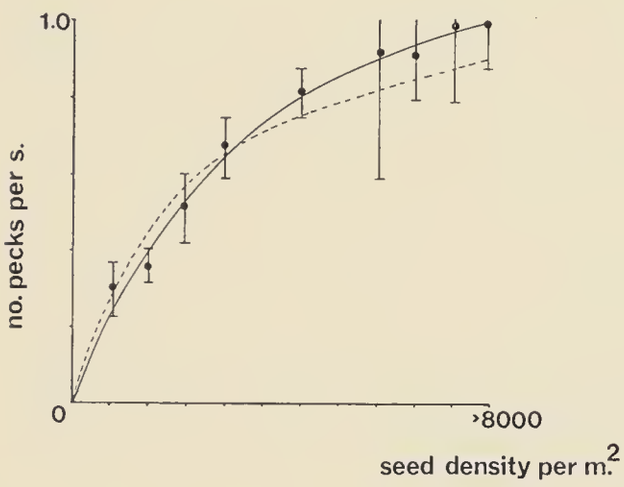

FIGURE 2. The relationship between pecking rate and seed density in sparrows feeding in a cattleshed. The distribution is not significantly different from that expected by Holling's Disc Equation with an empirically determined handling time of 1.02 ± .082 sec. (dotted curve) and therefore approximates to a Type 2 functional response. n = 54 feeding bouts. Curve fitted by eye.

In the cattlesheds, the budget was dominated by the functional response (HOLLING, 1959) of birds to variations in seed density. Pecking rate followed HOLLING's Type 2 response (Fig. 2) to seed density and birds spent most of the time during which they were not actually capturing food moving to a new, local feeding area; looking occurred only infrequently during a feeding bout and seldom interrupted a sequence of pecks. There was a relationship between each kind of behavior and flock size: pecking rate increased with flock size and both hopping and looking rates decreased. However, the relationship of flock size with all three kinds of behavior plateaued sharply and did not conform to a smooth curve (Fig. 3). Multiple regression analysis revealed that there was no correlation between the three kinds of behavior and flock size, per se, but that variation in the rates of performance of pecking and hopping correlated with seed density and the minimum temperature for the preceding 24 hours. Looking rate did not appear to be significantly influenced by any of the environmental factors I measured. The apparent relationship between flock size and the three kinds of behavior appeared to be due to a correlation between flock size and the proportion of its feeding time a bird spent in the patch of highest food density at a feeding site. The sharp plateaux were brought about by the fact that a certain flock size was reached above which most birds spent all their time in the best patch (Fig. 4).

In the open fields, however, flock size per se, and not seed density, appeared to be the most important factor governing the frequency with which each behavior was performed, and the relationship between any behavior and flock size did not plateau but described relatively smooth curves. Birds scanned for predators at a much higher rate than when feeding in the cattlesheds, and looking tended to interrupt sequences of pecks. By associating in flocks, birds appeared to be able to reduce their rate of scanning without significantly altering the overall rate of scanning by the flock as a whole (flock vigilance). A comparison of flock vigilance in both the cattlesheds and the open fields showed that vigilance was significantly lower in the sheds. This was due to the lower rates of looking and was reflected in the much shorter flight distances between myself, acting as an approaching terrestrial predator, and the feeding flock. In the open

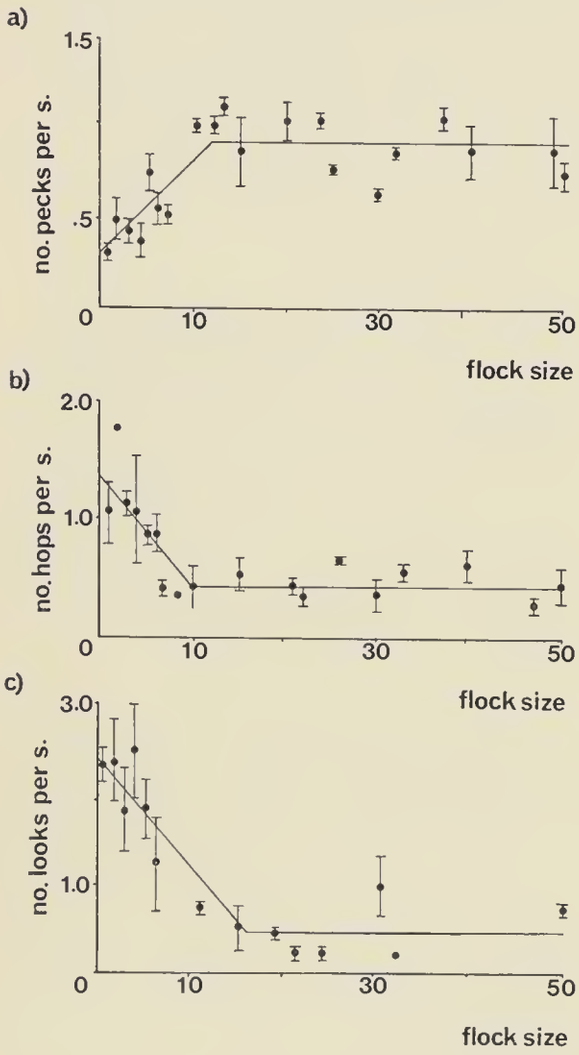

FIGURE 3. The relationship between the rates of pecking a), hopping b) and looking c) and the size of the feeding flock. The data in each graph are three parameter plots and best described by two intersecting straight lines. Lines are fitted by linear regression and the points of intersection determined by the 95 % concidence limits to the slope of the regression for the dependent part of the data. n = 279 feeding bouts.

fields, therefore, the higher level of flock vigilance was probably adaptive in that it facilitated the earlier spotting of predators. Variation in flock size did not have any effect on the length of the flight distance, so large flocks did not spot predators sooner than small ones. Food density and the minimum temperature for the preceding 24 hours, however, did affect length of flight distance; birds feeding on high densities of seed or after low overnight temperatures generally had short flight distances. This may have been due either to the increased role of pecking in the feeding budget or to a greater reluctance to leave a profitable feeding area. Looking rate increased significantly with distance of feeding from cover, and a possible explanation for the tendency

of birds to feed in larger flocks when far away from cover may have been that it enabled them to reduce the impact of a greater demand for vigilance on their rate of food intake.

The relationship between pecking rate and seed density in the open fields did not conform to HOLLING's Type 2 functional response but pecking rate did increase significantly with increasing seed density although it was not affected by variation in ambient or minimum temperature.

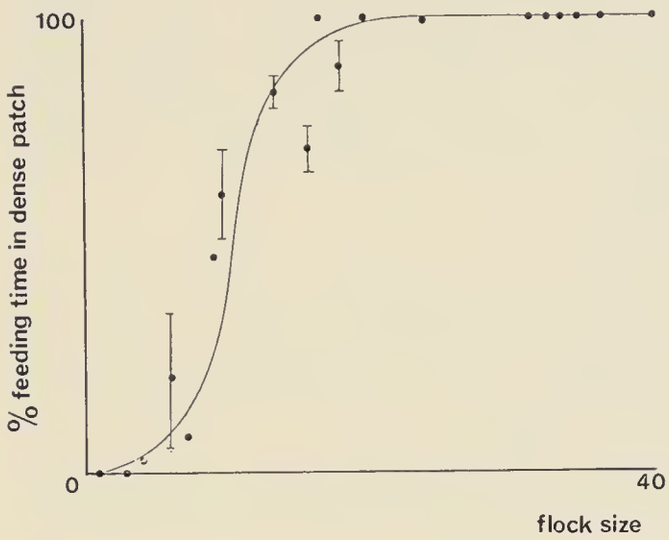

FIGURE 4. The relationship between the mean proportion of its feeding time a bird spent in the patch of highest density in the cattleshed environment and the size of the feeding flock. n = 38 feeding bouts.

Conclusions

The results of this study show that, within a population of birds, the organization of social behavior and of feeding may change between habitats. The way in which they change may reflect the differences in selective pressures which face birds feeding in different habitats. In the example discussed here, house sparrows responded to changes in the risk of predation by altering their degree of association into cohesive flocks and by placing emphasis on different kinds of behavior within their feeding budgets when they moved from one habitat to another. The changes conformed to those expected on the basis of individuals minimizing their risk of predation while maximizing their rate of energy intake.

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Attentiveness and Nesting Behavior of the Male and Female House Sparrow *(Passer domesticus)* in Wisconsin

C. A. North

Introduction

This study describes and evaluates the roles of male and female House Sparrows *(Passer domesticus)* in caring for their eggs and nestlings. Observations of nesting behavior were made during June and July, 1971. The study area, the nest boxes and the breeding season were previously described (North, 1970, 1972). The relatively large number of nest boxes in the study area probably provided a colonial nesting situation.

Methods

Nearly 500 hours were spent observing the behavior of pairs of breeding birds occupying 12 different nests. Nest boxes were located at heights of 3.7 and 4.6 m in tall trees that formed the border of a small street in the village of Coldspring, Wisconsin. The distance between trees varied from 6 to 20 m.

Observation periods were generally two hours in length. Observation times varied so that all daylight hours were included. Observers were equipped with 7 × 50 binoculars and stop watches.

The following information was collected for both male and female: (1) number of trips per hour; (2) time in the nest per trip; (3) time away from the nest per trip; and (4) general observations of the nesting behavior. This information was correlated with the stages of development of eggs or nestlings and time of day. A computer program was devised to synthesize this information for all of the breeding pairs and to organize it by day and by hour.

Egg laying and incubation

Eggs were generally laid in the early morning at the rate of one per day until the clutch was complete. During this time grass and feathers were still being brought to the nest by both the male and the female. However, only the female seemed to arrange the materials in the nest. Copulation was frequent during the egg-laying period and averaged 2—4 times per hour, but declined rapidly after completion of the clutch.

During the first two days of egg-laying the female averaged about 10 minutes per hour in the nest, while the male contributed about 5 minutes per hour. The time in the nest increased during the third and fourth days to an average of 16 minutes per hour for the female and 8 minutes per hour for the male. Clutches were completed on the fifth or sixth day depending on the number of eggs per clutch.

More intensive incubation generally began with clutch completion and continued until hatching. Both the male and female took turns in the nest during the daylight hours with the female roosting in the nest at night. The female was not fed in the nest

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by the male. She left the nest an average of 3.3 times per hour while the male made 2.5 trips per hour. The number of trips per hour for both sexes was fairly constant during most of the incubation period, but began increasing on the eleventh and twelfth days after clutch completion. The male seemed especially excited as hatching approached. Then both birds entered the nest more often and spent less time in the nest per trip (Table 1). Similar behavior was observed by Summers-Smith (1963).

The average time spent in the nest per trip by the female varied from a high of 13.2 minutes to a low of 7.0 minutes during the first 10 days of incubation and then declined rapidly on the following two days to less than 3 minutes on the twelfth day. The male spent increasingly longer spells in the nest until the ninth day, after which the time decreased to less than two minutes per spell on the twelfth day (Table 1). The average time in the nest per trip for the female (9.2 min.) was about double that of the male (4.5 min.). However, the male spent much longer periods away from the nest per trip than the female (22.3 minutes male to 10.4 minutes female). Deckert (1969) found sitting times to average 12.8 minutes, while Summers-Smith (1963) found that the female averaged 11.0 minutes and the male 8.9 minutes per spell.

Females frequently spent as long as 30 minutes on the nest per spell with the periods lasting as long as 56 minutes. Males seldom stayed in the nest as long as 20 minutes per spell but one remained in the nest for 43 minutes. The longest period that Deckert (1969) recorded was 41 minutes. Summers-Smith (1963) reported only three spells of more than 20 minutes during his study.

Nesting material was still being brought to the nest by both male and female during the entire incubation period. It consisted mostly of feathers but also of occasional pieces of grass.

Different pairs differed considerably in the percentage of time spent incubating eggs with variations from 41.2 % to 68.3 %. The average combined time spent on the eggs was 35.2 minutes per hour or 58.7 % (Table 1). This was much less than the 90 % observed by Summers-Smith (1963) in England and by Pinowski et al. (1972) in Poland. Deckert (1969) found the initial incubation time after clutch completion to be 50—60 % which gradually increased to 75 %. His pairs had incubation times which varied from 45 % to 90 %. One explanation for the lower incubation times in the present study may have been higher air temperatures. In June and July daytime temperatures in Wisconsin commonly reach 80° to 100 °F. Deckert (1969) found that temperature greatly influenced the amount of incubation by House Sparrows in Germany.

The female spent an average of about 25.7 minutes per hour (73 % of the total incubation time) on the nest during the incubation period (clutch completion to hatching). This time was fairly constant during the entire period and dropped to below 20 minutes per hour only on the twelfth day. The time per hour for the male was less than half that of the female averaging only 9.5 minutes per hour (27 % of the total incubation time). Summers-Smith (1963) reported the female doing 60.8 % of the incubation with the male doing 39.2 %. Daanje (1941) and Groebbels (1932) stated that males and females sit equally long on the eggs. The smaller proportion of the incubating done by the male in the present study was due in part to the presence of a bigamous male in the sample. If these bigamous nests were deleted, the male's role in incubation was increased to 34.7 %. The female seemed to spent proportionately more time in the nest during the

first part of the incubation period (day 1—6), while the male's time per hour increased during the last part of the period (day 7—12). The combined time per hour was fairly constant during each day of the entire twelve-day incubation period (Table 1).

The time per hour spent in the nest by the female during incubation was fairly evenly distributed throughout the day: 22 minutes per hour in the early morning (0500—1000), 27 minutes per hour in the mid-day (1000—1500), and 25 min. per hour in the late afternoon (1500—2000). The male distributed his time differently: 11 min. per hour in the early morning, 7 min. per hour in the mid-day, and 8 min. per hour in the late afternoon. The combined times in the nest were very constant during all three time periods (33—34—33).

At night incubation by the roosting female was continuous from about 20 minutes before sunset to 5—8 minutes after sunrise. The male made his last exit some 115 minutes before sunset, and entered for the first time in the morning 12—15 minutes after sunrise. However, there were wide variations according to the day and the breeding pair involved.

Table 1: Attentiveness by males and females during the incubation period

days	observation time (hours)	female trips per hour	female time in nest per trip (min) (max.)	female time in nest per trip (min) (avg.)	female time in nest per hour (min.)	male trips per hour	male time in nest per trip (min.) (max.)	male time in nest per trip (min.) (avg.)	male time in nest per hour (min.)	combined time in nest per hour (min.)	combined time in nest per hour (%)
1	14	2.0	32	12.8	25.6	2.9	14	3.6	10.4	35.6	59.3
2	8	3.7	31	7.0	25.6	2.3	8	2.0	4.6	30.5	50.8
3	17	2.3	43	13.2	30.4	2.0	15	4.0	8.0	38.4	64.0
4	12	2.6	48	12.2	31.7	1.0	21	4.3	4.3	36.0	60.0
5	22	2.8	40	11.5	32.2	1.4	12	3.3	4.6	36.8	61.3
6	22	2.7	33	10.3	27.8	1.8	28	5.3	9.5	37.3	62.2
7	20	1.9	48	11.7	22.2	1.9	27	9.8	18.6	40.8	68.0
8	26	2.5	34	9.9	24.8	1.5	56	7.0	10.5	35.3	58.8
9	26	2.5	32	8.5	21.3	2.2	25	6.1	13.4	34.7	57.8
10	12	3.3	18	7.1	23.4	2.3	31	5.7	13.1	36.5	60.8
11	12	6.3	24	4.2	26.5	2.8	9	1.9	5.3	31.8	53.0
12	8	6.8	12	2.5	17.0	7.6	4	1.6	12.2	29.2	48.7
total (avg.)	199	3.3		9.2	25.7	2.5		4.6	9.5	35.2	58.7

Hatching and the nestling period

Hatching took place from 9 to 14 days after clutch completion. In four (36 %) of the nests, all the eggs hatched on a single day. Two days were required for hatching in another four (36 %) of the nests, with three (27 %) of the nests taking more than two days. Only one clutch required four days for all six eggs to hatch, and these hatched on days 9, 10, 11 and 12. Seemingly, effective incubation was often initiated before the clutch was completed. All nests had 5 or 6 eggs per clutch. Summers-Smith (1963) also found that the hatching period may be spread over two or even three or four days.

The newly-hatched young were brooded by both parents for slightly more than 24 minutes per hour (40 % of the time) during the first three days. The parents spent an average of 21 minutes per hour (35 % of the time) in the nest during days 4 & 5. The brooding rate dropped considerably from day 5 to day 8 with very little brooding taking place after day 8, when the average time in the nest per trip dropped below one minute. The decreases in brooding times were also indicated by increases in the average numbers of trips per hour on days 4, 6 and 9 (Table 2). The female commonly roosted with the nestlings at night as she had with the eggs. During the day she did some 66 % of the brooding with the male making up 34 %.

TABLE 2: Attentiveness by males and females during the nestling period

days	observation time (hours)	female time in nest per trip (min.) (max.)	female time in nest per trip (min.) (avg.)	female avg. trips per hour	male time in nest per trip (min.) (max.)	male time in nest per trip (min.) (avg.)	male avg. trips per hour	combined trips per hour
1	14	39	2.4	7.7	7	1.4	4.1	11.8
2	16	30	2.6	5.5	24	2.0	5.3	10.8
3	14	21	2.7	5.3	12	2.4	4.1	9.4
4	18	30	2.4	7.2	12	1.6	3.7	10.9
5	3.5	9	1.5	8.0	18	1.3	5.3	13.3
6	30	12	1.1	10.5	9	0.9	6.4	16.9
7	22	15	1.3	10.3	13	1.1	7.9	18.2
8	22	19	1.1	9.8	5	0.7	6.8	16.6
9	24	15	0.9	14.8	14	0.7	15.8	30.6
10	26	12	0.7	15.9	3	0.6	9.7	25.6
11	24.5	3	0.7	15.0	3	0.9	7.7	22.7
12	12	8	0.7	14.9	3	1.0	2.0	16.9
13	18	7	0.6	21.1	1	0.5	2.4	23.5
14	12	10	0.5	19.8	5	0.6	6.6	26.4
15	0	—	—	—	—	—	—	—
16	10	1	0.5	6.5	1	0.6	2.3	8.8
total (avg.)	297.5			11.5			6.0	17.5

SUMMERS-SMITH (1963) found that brooding was fairly equally divided between the male and the female. His nestlings were brooded about 56 % of the time during the first two days with little brooding occurring after day 8. The warmer weather in Wisconsin probably reduced the amount of brooding in the present study. DECKERT (1969) noted that the brooding time was dependent on air temperature. There was no brooding after the second day in one of his study nests which was warmed by the sun.

The two parents together averaged 17.5 visits per hour during the entire nestling period. Significant increases in the number of trips per hour took place on day 6 and on day 9 with a drastic decrease on day 16 (Table 2). This feeding rate was considerably lower than the 23—25 feeds per day reported by SEEL (1966a) in England. However, SEEL deleted all nests where only one parent was usually present. If this was done in the present study, the total feeding rate was increased to 20.6 visits per hour. SUMMERS-

Smith (1963) observed an average of about 15 trips per hour, while Marples & Gurr (1943) found a rate of at least 20 visits per hour.

Most of the feeding was done by the females who made an average of 11.5 trips per hour as opposed to 6.0 trips per hour by the male (63.7 % by the female and 34.3 % by the male). Again, if the abnormal nests were deleted, the proportions became more even (56.3 % female to 43.7 % male). These figures are close to those observed by Summers-Smith (1963), who found the female doing 55 % of the feeding and the male only 45 %. Seel (1966a) stated that the male and female feeding rates were nearly equal.

The feeding rate for females showed a gradual increase from 7.7 times per hour on nestling day #1 to 21.1 on nestling day #13. The rate was still very high on day 14 but dropped drastically to 6.5 on day 16. The feeding rate for males was more variable. It increased from 4.1 times per hour on nestling day 1 to a high of 15.8 on day 9. Then it dropped rapidly to a low of 2.0 on day 12 rising slightly and remaining fairly constant thereafter (Table 2). Similar observations were made by Seel (1966b) in England.

Most trips to the nest after day 8 were very rapid, since by then most feeding was done without actually entering the nest box. Some feeding trips required as little as 3 seconds. The average time for all trips of less than a minute was about 16 seconds for females and 15 seconds for males. Both parents regularly removed fecal sacs and dropped them 30 to 70 feet from the nest tree.

The greatest combined number of trips per hour were made on day 9 by the pair in nest box #133. In this case the male made an average of 28.9 trips per hour and the female 21.5 trips per hour over a four hour observation period (0511—0900), totaling 50.4 trips per hour. On day 11 in the same nest box the female averaged 30.5 trips per hour over a two-hour observation period (0645—0845). This was the highest feeding rate observed for any one bird.

The average nestling day was separated into three feeding periods: 1) early morning (0500—1000), 2) mid-day (1000—1500), and 3) late afternoon (1500—2000). No great differences were found in the combined average feeding rate during these three periods. The greatest number of hourly trips was made in the early morning (21), with slightly fewer in mid-day (18) and late afternoon (17). The trips per hour by the male for all three periods remained stable (7—6—7), while the female made fewer trips after the early morning period (14—12—10). These findings differ from those of Summers-Smith (1963), who observed an average of 19.2 trips per hour in early morning, 9.2 during mid-day, and 15.7 in late afternoon.

The female generally first left the nest at about sunrise and returned for the last time in the evening about 16 minutes before sunset. The male first arrived at the nest about seven minutes after sunrise and made his last feeding trip 25 minutes before sunset. These times were quite variable. Seel (1966b) found in England that the female generally left the nest about 15 minutes before sunrise and returned for the last time some 20 minutes before sunset. The male made his first visit some 10 minutes after sunrise and his last visit some 30 minutes before sunset.

Most of the nestlings were fledged by nestling day 15, and none fledged later than day 16. The great reduction in feeding trips by both parents on day 16 may have been to encourage the young birds to leave the nest (Table 2). Fledging was observed in nest

box #133 where four nestlings had hatched on June 6 and 7. By June 14 (Nestling day #9) the adults began feeding the young without actually entering the nest. On June 18 (day # 13) the parent birds began spending much of their time just sitting in the entrance of the nest box. On day # 14 young birds were observed with their heads out of the entrance hole. Two of the nestlings left the nest unobserved on day # 15. On June 21 (16 days after the first egg hatched) the last two nestlings left the nest. One flew from the box at 05:53 and landed in the branches of the same tree some 10 feet above the nest. Afterwards, both parents kept landing at the nest box entrance seemingly trying to coax the remaining nestling out of the nest. At 05:59 the last nestling flew out of the nest box and landed in a nearby tree some 20 feet away.

Bigamy

Two of the 12 study nests were occupied by different females which were both mated with the same male. These nests were in nest boxes #131 and #135 which were located on different trees some eight yards apart. Clutches of six eggs were completed in box #135 on May 30 and in box #131 on May 31.

During incubation the male often landed on each box and looked in, but seldom actually entered either box. When he entered, he did not stay long in the nest (usually less than one minute per trip). In box #131 he made a total of 11 entries during 42 hours of observation time over a period of nine days. In box #135 he entered four times during 14 hours of observation over a period of four days. In all he spent an average of only 0.4 minutes per hour in nest #131 and 1.1 minutes per hour in nest #135. The longest single period spent in box #131 was 10 minutes and in box #135 7 minutes.

The male became much more active in both nests after the eggs hatched. Six young hatched on June 9—11 in box #135 and June 11 and 12 in box #131. After hatching was completed the male visited both nests fairly regularly to feed the nestlings. However, more of his time was spent with nest #135 than with nest #131.

For nest box #135 he made an average of 7.2 trips per hour during the nestling period. The female averaged 16.3 trips per hour. The trips per hour by the male increased until day # 9 (13.8 trips per hour), and then dropped to an average of only 1.5 trips per hour for the rest of the nestling period. The female made an average of 11 trips per hour until the male's feeding rate decreased on day # 10. From then on she averaged 22.2 trips per hour with a maximum rate of 24 trips per hour. The combined feeding rate never dropped below 18 visits per hour during any observation period, and reached a high of 26.2 visits per hour. Seemingly the female was able to successfully feed six nestlings with little help from the male after day # 10.

In nest box #131 the male was less active, but still managed to do some feeding during most observation periods. He started feeding only after all the young had hatched on day # 2. Thereafter he feed the nestlings during all but one of the 10 observation periods, averaging 2.5 trips per hour. The female averaged only 9.1 trips per hour during the entire nestling period. The combined (male plus female) feeding rate averaged 11.6 trips per hour, but dropped as low as 6.6 feeds per hour during one four-hour observation period. The highest combined feeding rate was less than 18 feeds per hour (17.8). All of the six chicks survived until day # 8 when three of them disappeared. It

seems possible that all six chicks could have been successfully fledged at this relatively low combined average feeding rate of 11.6 feeds per hour.

The incidence of bigamy in the House Sparrow may be more frequent than previously suspected and may often go unnoticed. WEAVER (1943), in his study in New York, found that the males seldom aided in incubation, and that it was difficult even to associate the correct male with its nest. Possibly several of these were bigamous males. SUMMERS-SMITH (1963) in England found that during one breeding season bigamy was very common. However, he attributed this to a temporary scarcity of males. DECKERT (1969) in Germany found bigamy to be prevalent during his study. Out of 19—23 nests in the colony, at least seven per year were occupied by females mated to bigamous males. One male was even paired with three nesting females. Instances of bigamous behavior have also been reported by BOXBERGER (1939) and by PEARSE (1940).

During the study seven of the twelve pairs successfully fledged young. The successful nests included the two occupied by the bigamous male and one in which the male may have been bigamous. In three of the five nests that failed, the female disappeared. In all cases in which the female disappeared the nest was abandoned by the male whether eggs or nestlings were present. In the one case where the male disappeared, the female continued feeding the nestlings which eventually fledged. Apparently a bigamous situation was no serious disadvantage to nesting success since the female seemed capable of incubating the eggs and caring for the nestlings with little or no help from the male.

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Changes in the Fat Reserves in Female House Sparrows *Passer domesticus* during Egg Laying

Luc Schifferli

Introduction

From studies on diurnal and seasonal changes in body composition of birds it is clear that body reserves play an important adaptive role in coping with periods that impose high energy demands, such as long distance migration or overnight survival in winter (review by King, 1972). It is well known that breeding (laying, feeding young) is an energy demanding period (Lack, 1968; Klomp, 1970; Perrins, 1970; Ryder, 1970; Ricklefs, 1974); thus changes in body reserves during the breeding season would be expected, as shown in two tropical species, the Red-billed Quelea *Quelea quelea* (Jones & Ward, 1976) and the warbler *Cameroptera brevicaudata* (Fogden, in Jones & Ward, 1976). These findings have been confirmed in the Reed Warbler *Acrocephalus scirpaceus* in temperate zones (Fogden, in Jones & Ward, 1976).

My study was designed to find out whether such changes in body reserves (fat and protein) could also be documented in the House Sparrow and to relate them to the breeding ecology (Schifferli, 1976). In this paper changes in the fat content of laying females are presented.

Methods

In the summers 1972—74 72 females were collected near Oxford, England, within two hours of sunset. Specimens were taken at nest-boxes which were checked at regular intervals. Before breeding started, females were mist-netted at random. In these females the measurements and fresh weights of their yolks in the ovary were compared with those of laying females collected at their nest-sites to establish when they would have started to lay. In the three days before the egg is laid its yolk grows rapidly and different stages show clear differences in weight and diameter.

All birds were plucked, dissected in detail and the food in crop, gizzard and alimentary canal removed. The corpses were dried to constant weight at 85 °C (dry weight), subsequently the fat extracted in a standard Soxhlet apparatus using chloroform as a solvent, and the lean dry weight obtained after the chloroform remaining on the specimens had been evaporated. The fat content was obtained by subtracting the lean dry weight from the dry weight.

Results

In my study area clutch-size varied between 3—5 eggs with an average of 4.2 (cf. Seel, 1968; Dawson, 1976). Four days before the egg is laid the yolk begins to form in the ovary (Figure 1, day —3). Since eggs are laid at daily intervals up to four yolks are formed simultaneously. In the early morning of the fourth day (day 0) the yolk is released from the ovary to the oviduct (ovulation), where the albumen and the shell of

Schweizerische Vogelwarte, CH-6204 Sempach, Switzerland

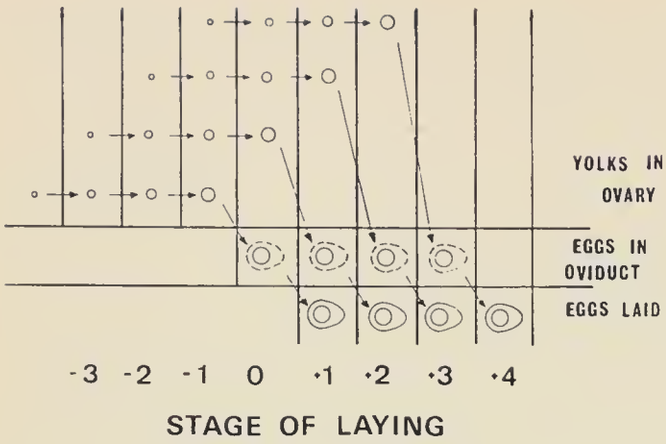

FIGURE 1. Schedule of the stage of laying for a female laying four eggs. Note: Yolks are ovulated at sunrise, after the previous egg has been laid. Females were collected in the evening; a female taken e.g. on day 3 had laid the third egg on the previous morning and had a fourth egg in the oviduct to be laid the following morning.

the future egg are produced (cf. STURKIE, 1965) before the egg is laid the following morning (day 1). As the females were taken in the evening, laying birds had an egg in the oviduct ready to be laid the next morning. Since material for eggs is synthesised already well before eggs are actually laid the "laying period" is defined in this paper as the interval from the beginning of yolk formation to the day the last egg is ovulated.

The decrease in the fat content of the female during the laying period is shown in Figure 2. In the three years under study the same trend could be shown; as there were no significant differences between years the data were pooled. From the regression line it may be seen that the fat reserves three days before the first egg is ovulated amount to about 2.07 g. This peak level decreased subsequently throughout the laying period, by about 0.15 g/day (slope of the regression line) reaching a minimum of 1.16 g by the time the last egg is ready to be laid in a clutch of four eggs. This represents a loss of 44 % (0.91 g) of the original fat reserves. If the female lays five eggs, a clutch-size found quite frequently, the loss amounts to 51 %.

Not all of the fat stored, however, is available for breeding activities. As the females were collected in the evening some of their fat reserves would have been metabolised during the night. The energy requirements for overnight survival were not measured in this study, but it is possible to calculate approximately how much energy would have been required. The basal metabolic rate was calculated, using the equation for passerines provided by ASCHOFF & POHL (1970), assuming an average roosting time of nine hours (mean night length April—June, the months most clutches are laid). The mean body weight of the laying females was 32.9 g (s.d. 2.15, n = 61) and thus about

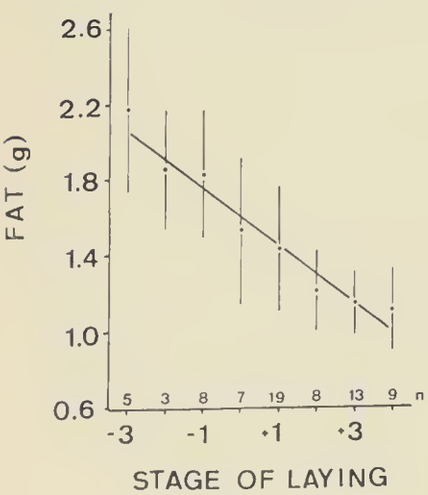

FIGURE 2. Total fat content of the female, in relation to the stage of laying. The regression equation is:
$y = -0.152 \times + 1.611$
s.e. of slope = 0.017, $t = 8.9$, $p < 0.001$.
Note: day 1 is the day the first egg is laid.

3.6 kcal would have been used for basal metabolism over this period. This is equivalent to 0.40 g of fat, assuming that all the energy used was gained from fat reserves.

In addition to this, a certain amount is an integral part of the cell structures (e.g. nerve sheaths) and cannot be withdrawn without interfering with their function (MASORO, 1967); it is therefore not available for metabolism (structural fat). 11 birds which were found dead, and had presumably died from starvation (very low in weight, no injuries) still had 0.25 g of fat. Assuming that this amount is non-metabolisable and that 0.4 g are required overnight only the fat accumulated above 0.65 g is available for breeding activities.

Adjusting the fat reserves accordingly we find that a female laying four eggs has some 0.51 g of fat left at the end of laying (1.16 g—0.65 g; Figure 2), and when a clutch of five eggs was laid her reserves were merely 0.36 g. Compared with the original reserves of 1.42 g three days before ovulating the first egg (2.07 g—0.65 g) this decrease in fat represents a loss of 64 % and 75 % in an "average" female laying a clutch of four or five eggs, respectively. Nevertheless, even the female with the lowest fat reserves (0.86 g—0.65 g) would certainly have survived the coming night. Hence the laying female draws heavily upon her fat, leaving little in reserve by the end of laying. However, she does not exhaust them below a level critical for survival.

The questions we have to consider now are: firstly, do the fat reserves reach their peak three days before the first egg is ovulated or well before laying? Secondly, is this peak attained by a marked and steep increase shortly before laying, or gradually over a prolonged period? A total of 76 females were caught in mist-nets at random between early April—about a month before breeding starts,—and early May, when breeding is underway. None of these females had laid in the season in which they were collected, as none had a brood patch which is developed during laying and can be recognised until the next moult (pers. obs.). Moreover, inspection of the ovary showed that none had initiated yolk formation which becomes clearly visible four days before laying. Thus, all these females were collected at least four days prior to laying, but no more precise information on the date at which they would have started laying is available. As such information is lacking we have to rely on the date of the start of laying in the sparrow population from which these prebreeding samples were taken. Such data were obtained by inspection of the nest-boxes. In different years laying started at different times of the season, and the dates at which the samples were taken had to be adjusted to make different samples comparable: the date by which 50 % of the females, breeding in nest-boxes in any one year, had laid their first egg was taken as "day L" (median date of laying; only clutches started before the 21st May were considered to avoid bias of replacement clutches and second broods). However, as the start of laying showed a considerable spread, I want to stress that the results presented here allow only tentative conclusions.

In Figure 3 the means of the total fat reserves have been plotted against the number of days before "day L". In addition the means of eight females which were probably about to initiate yolk formation when caught* and those that had started to form the yolk of the first egg (day —3, Figure 2) are given for comparison.

* These females had oviducts of a fresh weight of 0.5 g or more, typically found in females on day —3. Some of their follicles were slightly enlarged and showed trace of yolk.

The mean fat reserves of the females seem to decrease slightly from about 1.85 g four weeks before "day L" after which they stay more or less constant at 1.6—1.7 g (Figure 3). This amount is similar to that found in females which were very close to initiating yolk formation (1.68 g, s.d. 0.24, n = 8). Thus, the fat reserves seem to remain constant until very shortly before the female begins to deposit yolk in the ovary. By contrast, the females that had actually started forming yolks showed significantly larger fat reserves (2.17 g, s.d. 0.44, n = 5; $p < 0.02$). It seems therefore that a substantial quantity of fat is accumulated during a few days just prior to the start of yolk production and that the peak is reached about three days before the first ovulation.

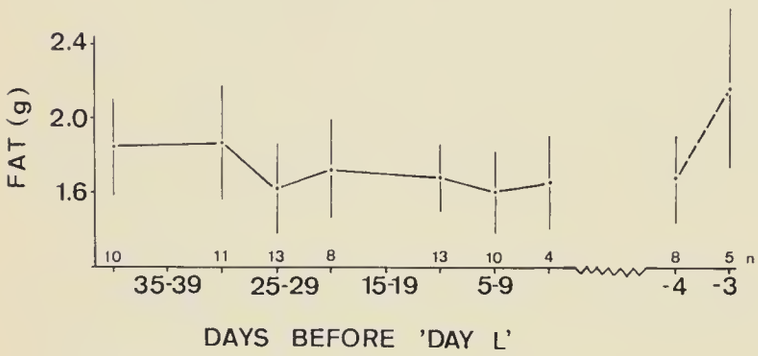

FIGURE 3. Total fat content of the female, in relation to the start of laying in the study populations. Means (± 1 s.d.) and sample sizes are shown.
Note: day 0 is the median date of laying (day L; cf. text).
day —4: females collected shortly before starting to form yolks
day —3: females collected three days before ovulating the first egg (from Figure 2).
The means of day —3 and —4 differ significantly. t = 2.7, 11 d.f., p = 0.02.

Discussion

The data on the body fat of the female provide some evidence reserves are accumulated very rapidly only shortly before the first yolks are formed in the ovary. In early House Sparrow broods DAWSON (1972) found a positive correlation between the maximum temperature and the number of clutches started a few days later, suggesting that the female might take advantage of favourable environmental conditions to build up her fat reserves. A similar pattern of fat deposition has been found in migratory species which deposit large quantities of fat within a short period immediately before migration (within 6—9 days in passerines; KING, 1972). The reason for a rapid instead of a slow and prolonged increase might be that additional energy is used to carry the extra weight of these reserves, as shown by an example: if a House Sparrow weighs 29 g it will need 26.1 kcal for daily energy expenditure (KING, 1974; cf. Table 1). With 1 g of additional reserves (i.e. body weight 30 g) it requires 26.7 kcal/day, or in 15 days 9.6 kcal more than without this fat. By metabolising 1 g of fat it will gain about 9.5 kcal, the same amount as it spent to carry this 1 g of fat for 15 days.

It seems most likely that fat reserves are used to cope with the energy demands of laying. To find out how important this contribution is we need some estimate of how much energy is required for egg laying. In the House Sparrow this has not been measured directly. Hence I shall attempt to obtain an indirect estimate. I stress that any such calculation is based on a number of assumptions which will inevitably result only in a rough approximation. Nevertheless, it will give some information as to whether the

fat reserves metabolised during the laying period are likely to contribute substantially or only marginally to the energy required by the laying bird.

Details of the energy budget are given in Table 1. Two different aspects are considered. First, some energy will be needed to synthesise the egg and oviduct material (total 19.5 kcal). Second, some additional energy will be needed to carry the extra weight of the oviduct, the yolks in the ovary and the egg in the oviduct ("reproductive material" in Table 1). This weight varies daily as the eggs are laid and also diurnally as the albumen of the oviduct egg is formed during the daylight hours. The females were collected in the evening when the egg is almost fully formed and the weight therefore at a maximum. The fresh weight of females collected during laying and yolk formation (days −3 to +4 in Figure 1) was on average 32.9 g (s.d. 2.15, n = 61). To obtain a mean, rather than a maximum weight, 1 g was subtracted (i.e. 1/2 of the albumen weight of 2.0 g, s.d. 0.17, n = 28). The "non-laying" weight of these females would have been 29.4 g (s.d. 1.98, n = 61), as obtained by subtracting the weight of all parts associated with laying from the live weight; thus, the female is about 2.5 g heavier because of laying. As the energy requirements depend on body weight, the energy demands of the laying female are increased by some 1.6 kcal/day, or 6.7 kcal during the laying period for an average clutch of 4.2 eggs. To sum up, the female will need some 29 kcal during laying, in addition to her daily energy expenditure.

During this period the female metabolises about 0.9 g of fat, equivalent to 8.6 kcal, or about 30 % of the energy used for laying. This is clearly a substantial contribution.

TABLE 1: Energy requirements for laying in the House Sparrow

			source
1. Energy for egg production			
1. Weight of clutch: 4.2 eggs, 2.73 g		11.5 g	DAWSON, 1972
2. Energy content of eggs: 1.16 kcal/g		13.3 kcal	KENDEIGH, 1973
3. Efficiency in converting energy: 77 %			BRODY, 1945 in KENDEIGH, 1973
4. Total energy required = 13.3 × 100/77		17.3 kcal	
2. For oviduct			
1. Fresh weight at the end of laying:	1.4 g		SCHIFFERLI, 1976
2. Fresh weight on day −3	0.6 g		SCHIFFERLI, 1976
3. Produced during laying	0.8 g		
4. Energy needed to form oviduct: 2.53 kcal/g fresh weight			RICKLEFS, 1974
5. Total energy required		2.2 kcal	
3. Extra energy needed because of the increased body weight during laying			
1. Body weight including "reproductive material":		31.9 g	this study
Daily energy expenditure (DEE):	28.0 kcal		KING, 1974
2. Body weight without "reproductive material":		29.4 g	this study
Daily energy expenditure:	26.4 kcal		KING, 1974
3. Extra energy needed: 1.6 kcal/day, total 9.9 kcal			
4. Total energy requirements			
1. Egg laying (1.4.)		17.3 kcal	
2. Oviduct (2.4.)		2.2 kcal	
3. Extra weight (3.3.)		9.9 kcal	
4. Total energy/clutch		29.4 kcal	

The female with the largest reserves had a fat content of 2.6 g on day 3 of which 1.95 g were available for her activity (structural fat and fat used for overnight survival comprising the remaining 0.65 g). Metabolising such reserves would cover over 60 % of the additional energy needed by the laying female. Thus, fat reserves are an appreciable benefit to the female.

Jones and Ward (1976, and in press) stress the high demands of protein, especially when albumen for the egg is formed. They suggest that the female *Quelea quelea* search specifically for insects to obtain protein, temporarily neglecting the energy intake which is covered by metabolising fat reserves.

Pinowska (1976) showed a decline in the fat reserves of female House Sparrows breeding in Poland, but only in those laying six eggs. My own data are inadequate to separate females laying different clutches, as the prospective clutch-size can only be determined on day 0 — day 1. Nevertheless, females laying different clutches were equally represented in my sample. In the Polish populations fat was accumulated very rapidly, which agrees with my findings, but the peak was attained on the day the first egg was laid. This differs from my results for unknown reasons.

Information on other bird species suggest that body reserves are commonly used during laying. A large number of sea birds, arctic geese and waders arrive on their breeding grounds when feeding conditions are poor and/or they spend long periods at their future nest-sites. Thus, food intake is much reduced and body reserves are an important source of energy and materials for prelaying activities and forming the eggs (Barry, 1962; Fisher, 1967; Frings & Frings, 1961; Hanson, 1962, 1965; MacLean 1969; Richdale, 1947; Ryder, 1970, 1975; Warham, 1974).

In the Red-billed Quelea Jones & Ward (1976) found a marked fall in the fat and protein level during laying which they associate with the high protein demands imposed on the laying female. Similar findings are also reported by Fogden (in Jones & Ward 1976) in the Reed Warbler and in *Cameroptera brevicaudata.* In the House Martin *Delichon urbica* females dropped in fat reserves between arrival and the end of laying (Lyuleeva, 1962) and Sand Martins *Riparia riparia* lost more weight during laying than could have been attributed to changes in the weight of the reproductive organs alone (Stoner, 1936; Petersen, 1955).

However, there are bird species that can apparently maintain their body condition despite laying eggs. No changes could be detected in the female Chestnut-breasted Finch *Lonchura castaneothorax* (Perrins, pers. comm.). The reason why the female can cope with laying eggs from the daily food intake is unknown. Moreover, the female Blue Tit *Parus caeruleus* also maintained a fairly constant fat level (Perrins, pers. comm.). This species lays a clutch 2—3 times larger than most passerines (Lack, 1966). If the female were to store similar amounts of fat reserves as the House Sparrow, their contribution over the prolonged laying period would be very small. In this species the male has an important function in feeding his female prior and during laying (so-called courtship feeding; Lack, 1940; Andrew, 1961; Krebs, 1970). Royama (1966) estimated that the additional food the female obtained from her male might be sufficient to form one egg per day. This is clearly more than the female House Sparrow is likely to gain from metabolising her fat reserves. Royama suggested that the female might not be able to form her eggs without the help from her male. Courtship feeding does not occur in the species mentioned before.

To summarise, this study has shown that female House Sparrows deposit large fat reserves shortly before laying. They are metabolised during laying and contribute some 30 % to the additional energy required for producing eggs.

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Multiple Regression Analyses of Mid-Winter Lipid Levels in the House Sparrow, *Passer domesticus*

Charles R. Blem

Introduction

The close association of the House Sparrow with man has provided both the opportunity and the justification for extensive analysis of the ecophysiology of this bird. Few species of wild birds are so abundant, widely distributed and economically important. Within this context, the ecological energetics of House Sparrows has been intensively studied by many students (see Barnett, 1970; Blem, 1973, 1974, 1975a, 1975b, 1976a, 1977; Hudson & Kimzey, 1966; Kendeigh, 1944, 1949, 1973, 1976; Kendeigh & Blem 1974; Myrcha et al., 1973; Weiner, 1973), and the ability of the species to adjust and adapt seasonally and geographically is now fairly well known.

A significant component of the annual energy expenditure of House Sparrows is included in daily lipid cycles, particularly during the winter. Although mid-winter fattening appears to be a widespread phenomenon in small birds of the temperate zone, it is well known for only a small number of species (for reviews see King, 1972; Blem, 1976b). The magnitude of deposition and amplitude of diurnal lipid cycles appear to increase with severity of weather conditions and both reach highest levels in mid-winter (usually January) with some precision. The lipid reserves remaining after a long winter night's fast is generally sufficient for only a few hours of morning activity, even during phases of the annual cycle when ambient temperature and photoperiod are favorable for acquisition of surplus energy. This suggests that lipid depots are not maximized at all times of the winter. This may be due to selection of individuals with appropriate wing-loads (Blem, 1975a). Large amounts of lipid would be advantageous in survival of weather extremes, but would be a locomotor hindrance in predator avoidance. Also, the activity required to accumulate energy reserves must strike a selective balance between the benefits accrued and the risks of exposure and travel.

Beginning with research by King & Farner (1966) and Evans (1969), statistical models of the relationship between environmental variables and the amount of lipid reserve have begun to emphasize the importance of climatic variables as both proximate and ultimate factors (also see Vincent & Bedard, 1976). To date, such analyses have involved only simple regression techniques or highly restricted multivariate models involving only a few or single independent variables. The present study attempts to expand this technique by including a wide variety of environmental and morphometric variables in the same analysis. In addition, the importance of morphometric variables in relation to lipid reserves is compared to the daily influence of environmental variables. In this way it is hoped that the relative importance of various proximate and ultimate factors to lipid deposition may be determined and that models capable of accurately predicting lipid levels in living birds may be developed.

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Methods

One hundred House Sparrows were mist-netted at several localities in and near Richmond, Virginia from November, 1975 through March, 1976, and 21 more were collected in a similar period in 1976—1977. Birds were captured at a wide variety of time in daylight hours and an effort was made to distribute captures so as to represent the widest variety of times throughout the day. No bird was in a net more than five minutes before being sacrificed by thoracic compression. Fresh post-mortem weights were obtained in the field on a triple-beam balance and checked later in the laboratory with an electronic balance. Fat class was visually assessed using the system of HELMS & DRURY (1960). Wing chord, tarsus and culmen lenghts were measured with a vernier caliper. The feathers were manually removed from each carcass and all specimens were frozen until the lipid extraction procedure was begun. After being freeze-dried to constant weight, carcasses were extracted in a 5 : 1 mixture of petroleum ether and chloroform in soxhlet refluxing extractors, redried and the lipid content was considered to be the weight lost during extraction. The weight of the remaining material represents lean dry weight.

Multiple regression equations predicting lipid content of whole sparrows were generated using a large set of independent variables, including both carcass components and weather data (Table 1), associated with the 1975—1976 sample of sparrows. Environmental data were obtained from the records of the Richmond, Virginia station of the United States Weather Bureau. Not all the variables could be simultaneously included, so large subsets were analyzed (e.g., all temperature variables, all body components, all significant variables in previous models) and the variables that were obvi-

TABLE 1: Independent variables included in analyses of mid-winter fattening of the House Sparrow

I. Morphological variables	II. Temporal variables	III. Weather variables
A. Body weight (g)[1]	A. Julian date[2]	A. Dry-bulb temperature[5]
B. Wing length (mm)	B. Month[3]	B. Long-term (35-year) average dry-bulb temperature[5]
C. Culmen length (mm)	C. Hours after sunrise[4]	C. Wet-bulb temperature[5]
D. Tarsus length (mm)	D. Hours before sunset[4]	D. High and low dry-bulb temperatures
E. Sex (♂ = 1, ♀ = 2)	E. Eastern standard time[4]	E. High and low wet-bulb temperatures
F. Fat class	F. Photoperiod (hours of light)[4]	F. Relative humidity
		G. Barometric pressure[5]
		H. Precipitation[5]
		I. Wind velocity
		J. Percentage sunshine
		K. Chill factor[6]

[1] Also body weight expanded to the exponential powers 0.67, 0.72, and 0.75.
[2] Adjusted so that days from November through March are numbered consecutively.
[3] November = 1, December = 2, January = 3, February = 4, March = 5.
[4] Quantified to the nearest 0.1 hour.
[5] Including the day of capture (D), day before capture (DB), and day after capture (DA).
[6] Calculated by method described by SIPLE & PASSEL, 1945.

ously important retained in subsequent models unless eliminated by the regression procedure (see discussion below). The sparrows collected in 1976—1977 were used as an independent check of the accuracy of equations developed for sparrows from 1975—1976, and to test for variation between years. Analysis of variance was used to examine monthly and sexual variation in lipid content, lipid index, body weight, lean dry weight and wing length. A significance level of 5 % ($P < 0.05$) was used in all tests.

Results

There is no significant sexual or monthly difference in body weight or lean dry weight of sparrows collected during this study. Wing length varies significantly with sex ($F = 60.4$) and month of capture ($F = 5.9$). There is a significant sexual difference in quantity of lipid ($F = 5.0$) and lipid index ($F = 6.3$), but no significant monthly difference in either variable (Table 2).

Table 2: Body weight and lipid content of House Sparrows collected at Richmond, Virginia. Lipid indices are calculated as lipid/lean dry weight. All values are means ± one standard error.

Month	Sex	N	Weight (g)	Lean dry weight (g)	Lipid (g)	Fat class	Lipid index
November	♂	13	29.2±0.5	7.3±0.1	1.5±0.1	1.9±0.2	0.20±0.01
December	♂	17	28.5±0.4	7.0±0.1	1.3±0.1	1.8±0.2	0.18±0.01
January	♂	7	28.1±0.7	6.9±0.2	1.4±0.2	1.8±0.3	0.21±0.02
February	♂	14	27.4±0.4	6.8±0.1	1.4±0.1	2.0±0.2	0.20±0.01
March	♂	11	28.0±0.4	6.9±0.1	1.4±0.1	1.9±0.2	0.19±0.01
November	♀	6	26.1±0.5	6.5±0.1	1.5±0.1	2.1±0.2	0.22±0.01
December	♀	10	28.0±0.6	6.9±0.2	1.5±0.1	2.1±0.2	0.22±0.02
January	♀	3	28.2±1.1	6.8±0.3	1.5±0.1	2.2±0.2	0.22±0.02
February	♀	7	28.8±0.5	7.2±0.3	1.5±0.1	1.9±0.3	0.19±0.02
March	♀	12	27.8±0.5	6.8±0.1	1.5±0.1	1.9±0.2	0.23±0.01

Since a large number of equations, utilizing a wide variety of variables, were generated, several of the independent variables were significant in one model or another. In addition, the interactions between some variables proved to be even more influential components of equations. The most important single variables in the prediction of lipid content are fat class and body weight (the latter is slightly better as judged by improvement in the coefficient of determination (R^2) if adjusted to the exponential power 0.72). The "best" predictive model using all independent variables available to me is:

$$\text{Lipid (g)} = 0.967 + 0.129 \text{ body weight}^{0.72} - 1.206 \text{ fat class} + 0.071 \text{ sex (fat class)} - 0.027 \text{ hours before sunset} \quad (1)$$

As judged by the partial sum of squares, body weight (1.65), and fat class (1.00) are more important than sex (fat class) (0.37) and hours before sunset (0.39) in the equation. The coefficient of determination is 0.83.

Models using only environmental variables are much poorer predictors of lipid content. For example, the "best" model using temperature variables only is:

Lipid (g) = 1.320 — 0.052 dry-bulb temperature (D) + 0.035 dry-

bulb temperature (DA) + 0.056 wet-bulb temperature (D) — 0.034 wet-bulb temperature (DA), R 2 = 0.25 (2)

The "best" model using all environmental (temporal and weather) variables is:

Lipid (g) = 2.473 — 0.212 photoperiod + 0.044 hours after sunrise — 0.044 dry-bulb temperature (DB) — 0.612 dry-bulb temperature (D) + 0.095 dry-bulb temperature (DA) + 0.053 average dry-bulb temperature (D) + 0.330 high dry-bulb temperature + 0.337 low dry-bulb temperature — 0.131 wet-bulb temperature (DA) — 0.052 wind velocity, R 2 = 0.40 (3)

Using the appropriate environmental data, predicted lipid levels were obtained from equation (1) for sparrows collected in the winter of 1976—1977. These differ from empirically determined values by a mean absolute difference of 0.16 g. This difference is greatly inflated by two extreme values. Fifteen of the 21 estimates differ from actual lipid levels by less than 0.16 g. The mean difference, sign included, is — 0.004 g ± 0.04 g (range: — 0.44 to 0.41 g).

There is no significant difference between the lipid levels of sparrows collected in different years. When the sparrows from both years are pooled, the "best" equation is similar to equation (1):

Lipid (g) = 0.929 + 0.138 body weight 0.72 — 1.280 fat class +0.059 sex (fat class) — 0.022 hours before sunset, R 2 = 0.81

Discussion

Investigations of phenomena related to a potentially large set of independent variables have been greatly assisted by modern multivariate techniques implemented by electronic computers. One statistical technique that has found much recent use is multiple regression analysis. This is a technique for partitioning the variation around a dependent variable among all recognized independent variables in the model. This technique is used when the researcher hopes either to select those variables which best explain the process under investigation or to obtain a predictive equation. In the former case, variables that appear important when analyzed individually may be affected by the simultaneous analysis of other factors if the method of computation is not chosen judiciously. In searching for an appropriate predictive equation, regression on a subset of the variables may be preferable to an equation which contains all of the variables but is unstable. There are some inherent weaknesses of such models. There is no assurance that all significant independent variables have been included. If such variables are added to a later model, one may find that the precision of prediction is greatly increased and independent variables previously thought to be important are now less important or are rendered insignificant. The multiple regression equation in general must be viewed as indicative of the relative statistical importance of independent variables, not their absolute biological importance.

Criteria available for selecting the "best" regression equation are numerous. Most are functions of the residual sum of squares for subsets having the same number of independent variables (HOCKING, 1972). The usual procedure is to compute all possible regression equations and search for those having the minimum residual sum of squares among all subsets of the same size. For n variables, the number of possible regression

equations is 2 n — 1 and the number of operations required to invert the moments matrix associated with each subset is proportional to n 3 (Furnival & Wilson, 1974). Alternatively, one can divise a selection criterion for adding variables to or dropping them from the analysis. These methods select a variable for addition or deletion based on the amount of change in the coefficient of determination (R 2). These methods include forward selection ("step-up"), backward elimination ("step-down"), stepwise selection (a combination of the first two), maximum R 2 improvement, minimum R 2 improvement, and branch and bound techniques (Furnival & Wilson, 1974). The various merits of these techniques have been widely examined (e.g. Mantel, 1970; Zar, 1974), but my choice from experience (Blem, 1976a) is the stepwise maximum R 2 improvement model developed by Goodnight (see Barr et al., 1976). This technique finds the "best" one-variable model first. This is the one-variable equation which produces the maximum R 2. Once that model is found, the variable which produces the next greatest increase in R 2 is chosen and added to the model. Each of the remaining variables is compared to those already in the model to determine if replacing the included variable would result in a larger R 2. After all possible comparisons have been made, if a switch of variables has been indicated, it is made. The process continues until it is determined that no exchange of variables could increase R 2, and the resulting model is the "best". The technique selects, third, fourth and further variables for inclusion in the same manner.

In the present study, this regression process results in the virtual elimination of environmental variables from the model when morphometric variables are included. This does not mean that the environment is totally unimportant to the level of obesity of sparrows, but does emphasize the significance of sex and variation in body weight to the prediction of fatness of these birds. Lipid content of female House Sparrows appears to be greater than that of males (Blem, unpublished; the present study) and larger birds tend to be more obese (also see Blem, 1973). The relative importance of the subjective determination of fat class emphasizes the usefulness of this technique in roughly assessing lipid reserves.

The relative ineffectuality of environmental variables is illustrated by the much lower R 2 values associated with models excluding morphometric variables. Although the "best" environmental model includes ten variables deemed statistically significant, none of them are clearly more important than the rest, although temperature variables are prominent. The effect of most environmental variables upon mid-winter energy reserves of House Sparrows and other small passerines has been largely neglected, but many studies have suggested previously that increased body weight, visible subcutaneous fat or extractable lipid is correlated with temperature. For example, the magnitude of lipid depots in House Sparrows collected at night during mid-winter is known to increase with latitude and is correlated with the temperatures of the collection locality (Blem, 1973). These reserves appear to increase only gradually from summer to winter (Barnett, 1970), but monthly data from extremes of the range of the House Sparrow are not available. The difference between summer and winter reserves is probably much greater at higher latitudes (see Blem, 1973), and presumedly, fattening is much more extreme in the autumn at such sites. King & Farner (1966) demonstrated a positive relationship between lipid reserves and air temperature in the White-crowned Sparrow *(Zonotrichia leucophrys gambelii)*. However, the role of temperature as either a proxi-

mate or ultimate factor (or both) in determining the level of obesity is not well known. Evans (1969) found that lipid content of Yellow Buntings *(Emberiza citrinella)* is not related to actual temperatures around the day of capture, but is closely correlated with the long-term average temperature of the collection date. This implies that temperature is an ultimate selective factor in determining the level of lipid reserves rather than a proximate one. This finding has apparently not been supported by the few studies of other species (e.g. Vincent & Bedard, 1976; the present study), but this may be the result of the wide variety of mid-winter adaptational strategies available to small birds (Blem, 1976b; King, 1972; King & Farner, 1966; Vincent & Bedard, 1976). In fact, some small passerines of high latitudes appear to show little, if any, winter fattening (see King & Farner, 1966). In the present instance, although long-term average temperature is a significant variable (but of relatively minor importance) in the model using all environmental variables, it is only one of seven temperature variables retained. Correlations between the various temperature measurements tend to decrease the importance of any single temperature variable, but no single temperature demonstrated correlation coefficients as large as several other environmental and morphometric variables. Additionally, when only temperatures are used in the analysis, long-term average temperatures become nonsignificant. The apparent low sensitivity of House Sparrows to temperature and other environmental variables may be due to the close association with man, behavioral adjustments in relation to temperature extremes (see Beer, 1961) or the fact that the sparrows analyzed were taken from an intermediate location in the range where acclimatization to extreme temperature is only relatively minor.

Relatively precise models for predicting lipid levels in House Sparrows were generated in the present study. Not only is the R 2 in the "best" overall model relatively high, but the ability of this equation to predict values for an independent sample of sparrows is fairly good. To my knowledge, no studies have previously analyzed the relationship of a very large set of environmental variables to lipid reserves of a vertebrate (but see Vincent & Bedard, 1976). Such an approach will not help to separate proximate from ultimate controls, but should help to isolate important factors influencing obesity. Furthermore, the technique promises to provide a method for accurately predicting the lipid reserves of living birds and should be usefull to ornithologists doing field work. We are now pursuing further investigations in which such analyses are being expanded and applied to the migratory White-throated Sparrow *(Zonotrichia albicollis).*

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Adaptive Responses in Skeletal Characters of the New World Population of *Passer Montanus*

Jon C. Barlow

Introduction

As with the House Sparrow *(Passer domesticus)* the European Tree Sparrow *(P. montanus)* has been introduced several times outside its normal range. Successful importations of *P. montanus* have been made into Australia, the Philippines and North America. The House Sparrow, released by the hundreds in North America in the 1850s, and now comprising a population of several billion birds, was soon spreading rapidly across the continent. In contrast the present American population of *P. montanus,* numbering fewer than 100,000 individuals, stems from a release of 20 birds from Germany at St. Louis in 1870. I have previously discussed the history of the establishment of *montanus* in Missouri and Illinois (Barlow, 1967; Barlow, 1973) as has Anderson (1973).

In view of the rapid differentiation demonstrated between New World and European populations of *P. domesticus* (Johnston & Selander, 1964, 1971; Selander & Johnston, 1967) and the different population histories of the two species of *Passer* in America it seemed instructive to investigate the possibility of divergence between contemporary Illinois and German populations of *montanus* and the implications thereof for contemporary evolutionary thought.

Previous study of skin characters

Specimens of both sexes and age classes (adults/subadults) of *montanus* taken at Ludwigsburg, Germany, and in Illinois near Belleville, St. Clair Co., Roodhouse, Greene Co., and Jacksonville, Morgan Co. in autumn, and thus in fresh feather, were compared with respect to standard mensural characters (bill width, culmen-nostril, wing-chord, tail and tarsus lengths and weight) and color (chroma [x], hue [y] and brightness [Y]) of crown and breast plumage. No differences were detected in a spectrographic assay of color, and among adults only tail length differed significantly (longer in Illinois males than in German males) among mensural characters (Barlow, 1973).

Significant difference in wing-length variance between adult Illinois (smaller) and German (larger) females was interpreted as possibly reflecting reduced genetic variability in the Illinois birds as a function of the smaller size of the founder population and subsequent isolation from Old World birds. Tail length differences might be genetic or ecotypic in response to differential environmental abrasiveness at the two localities.

Methods

Johnston & Selander (1971) showed in *P. domesticus* that phenetic differences in skeletal characters did not necessarily parallel trends in feather characters among local-

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ities. I wished to determine if *P. montanus* resembled *P. domesticus* with respect to the developmental history of skeletal characters and to assess the nature of any divergence between German and Illinois birds. Therefore I compared by univariate analysis (UNIVAR) sample means of adult German (Ludwigsburg) males (n = 11) and females (n = 12), and Illinois (near Roodhouse) males (n = 29) and females (n = 14) for 16 skeletal dimensional characters. Included were lengths (to the nearest 0.05 mm) of skull (SKLL), premaxilla (PRMX), dentary (DENT), mandible (MNDB), humerus (HUML), ulna (ULNA), coracoid (CRCD), sternum (STRL), keel (KEEL), femur (FEML), tibiotarsus (TBTR) and tarsometatarsus (TRMT); widths of skull (SKLW), narial (NARW), bones and femur (FEMW); and sternum depth (STRD) as measured in *P. domesticus* by Johnston & Selander (1971). Gabriel's sums of squares simultaneous test procedure (SS-STP) was calculated on ranked means of all characters among which significant differences occurred. UNIVAR also calculated a variety of statistics of which standard error and coefficients of variation were of special interest in this study. A stepwise discriminant function analysis (SDFA) was used to determine which characters significantly separated the samples from each other and as a possible indicator of the magnitude and direction of any divergence in the American population of *montanus*.

Results

Univariate analysis

Significant differences among means were demonstrated for 13 of 16 characters (Table 1). In each of the 13 significant comparisons Illinois females were at least significantly smaller than German males. German males were largest 11 times or not signifi-

Table 1: Means plus one standard error and results of SS-STP for 16 bony characters of adult *P. montanus* from Germany and Illinois

Character	German, ♂♂ (n = 11)	German, ♀♀ (n = 12)	Illinois, ♂♂ (n = 29)	Illinois, ♀♀ (n = 14)
1. Premaxilla length**	11.63 ± 0.086	11.59 ± 0.092	11.38 ± 0.071	11.07 ± 0.134
2. Narial width ns	0.92 ± 0.021	0.91 ± 0.027	0.90 ± 0.013	0.89 ± 0.134
3. Skull width**	14.85 ± 0.095	14.75 ± 0.087	14.70 ± 0.048	14.46 ± 0.071
4. Skull length**	27.34 ± 0.099	27.30 ± 0.016	26.97 ± 0.091	26.52 ± 0.014
5. Dentary length ns	5.37 ± 0.058	5.33 ± 0.056	5.24 ± 0.042	5.14 ± 0.086
6. Mandible length**	18.86 ± 0.087	18.39 ± 0.016	18.34 ± 0.075	18.12 ± 0.017
7. Coracoid length**	17.80 ± 0.076	17.44 ± 0.017	17.36 ± 0.054	17.14 ± 0.011
8. Sternum length***	21.59 ± 0.092	21.18 ± 0.010	21.04 ± 0.020	19.77 ± 0.041
9. Keel length***	20.64 ± 0.129	19.83 ± 0.104	19.81 ± 0.207	18.60 ± 0.182
10. Sternum depth***	10.25 ± 0.101	9.82 ± 0.146	9.72 ± 0.085	9.12 ± 0.101
11. Humerus length***	17.22 ± 0.087	17.02 ± 0.042	16.95 ± 0.062	16.56 ± 0.092
12. Ulna length***	19.09 ± 0.071	18.78 ± 0.002	18.69 ± 0.114	18.03 ± 0.116
13. Femur length***	16.76 ± 0.056	16.61 ± 0.071	16.60 ± 0.080	16.27 ± 0.123
14. Femur width ns	1.19 ± 0.016	1.19 ± 0.011	1.19 ± 0.011	1.17 ± 0.013
15. Tibiotarsus length***	25.86 ± 1.181	25.61 ± 0.105	25.47 ± 0.127	24.82 ± 0.195
16. Tarsometatarsus length**	17.56 ± 0.082	17.46 ± 0.070	17.34 ± 0.170	16.98 ± 0.131

** $P \leq 0.01$; *** $P \leq 0.001$

cantly smaller than German females or Illinois males in the other three instances where significant differences existed. For five characters (PRMX, SKLL, MNDB, CRCD, STRD) the order of ranked means was German males ⟩ German females ⟩ Illinois males ⟩ Illinois females. For MNDB, KEEL, and STRD Illinois males, were significantly smaller than German males, but not German females. For STRL, HUML, ULNA, FEML, TBTR, TMTR, and KEEL, Illinois males were slightly, but not significantly larger than German females. For KEEL German males were significantly larger than the other three samples. No significant differences existed among samples for NARW, FEMW, or DENT. In general, most characters of German males were largest, and of Illinois females smallest; German females and Illinois males were intermediate and always about the same size, but with the latter slightly, but not significantly, larger in 7 of 13 comparisons. Grouped by function, significant differences exist in the trophic apparatus (PRMX, SKLW, and SKLL) between German adults and Illinois females and between the latter and German males for MNDB, also associated with food getting. PRMX, MNDB, and DENT are directly associated with picking up and husking seeds, whereas SKLW and SKLL represent bony structures to which muscles associated with feeding are attached and thus size differences in the latter may be an indirect measure of feeding differences. In flight characters Illinois females are significantly smaller than German males in CRCD and significantly smaller than both German adults in STRL and STRD and from all other adults in KEEL, HUML and ULNA. Illinois females are also significantly smaller than all males in FEML, TBTR, TRMT, which are characters involved in both foraging and perching.

TABLE 2: Intercontinental comparison of character variation in *P. montanus:* Intralocality variation — coefficient of variation

Character	German ♂♂	German ♀♀	Illinois ♂♂	Illinois ♀♀
Premaxilla length	2.46	2.75	3.34	4.54
Narial width	10.03	7.11	7.48	7.99
Skull width	1.96	2.22	1.77	1.82
Skull length	1.20	2.01	1.82	2.03
Dentary length	3.60	3.61	4.28	6.27
Mandible length	1.54	3.03	2.19	3.43
Coracoid length	1.14	3.35	1.67	2.38
Sternum length	1.41	1.42	2.57	1.55
Keel length	2.07	3.62	2.82	3.66
Sternum depth	3.28	5.16	4.71	4.18
Humerus length	1.67	1.27	1.50	2.07
Ulna length	1.23	2.11	1.78	2.41
Femur length	1.41	1.66	1.79	2.84
Femur width	4.37	3.32	5.07	4.00
Tibiotarsus length	2.32	1.69	2.21	2.93
Tarsometatarsus length	1.54	1.54	2.16	2.88

Examination of coefficients of variation (Table 2) reveals few instances of either intra population or interpopulation variability. Relatively high CV's are found in Illinois females for PRMX, DENT, and MNDB which may reflect some increased variability in diet or rate of bill growth in that sample. In general interpopulation variability

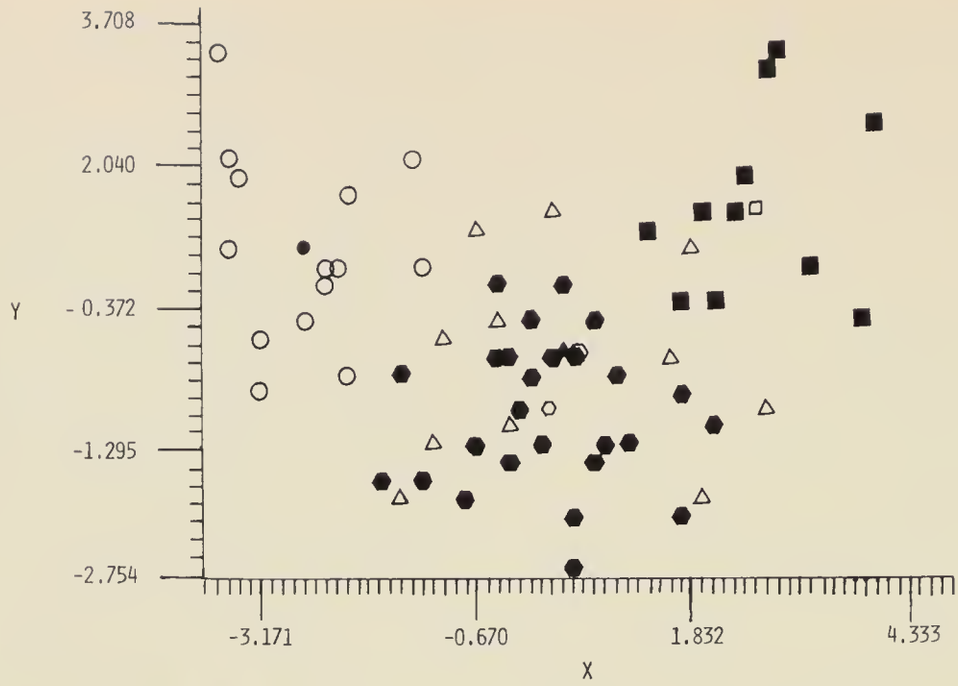

FIGURE 1. Canonical variates analysis of discriminant function scores for German ♂♂ (■) and ♀♀ (△) and Illinois ♂♂ (⬢) and ♀♀ (○). Sample means are indicated by smaller circles and polygons as follows: German ♂♂ (□); German ♀♀ (▲); Illinois ♂♂ (⬡); Illinois ♀♀ (●).

is homogeneous and there is no evidence of decreased variability which might accrue to the small size of the founder population. Commonality of variability has previously been noted between North American and European *domesticus* (JONSTON & SELANDER, 1971).

Multivariate analysis

The stepwise discriminant function analysis computed discriminant scores for all characters over OTU's (Operational Taxonomic Units), arranging characters in descending order of their ability to discriminate among OTU's and at the same time calculated F-values so that significant discriminators were identified. Then a canonical variates analysis of the discriminant function scores showed the degree of separation of the four OTU's in a bivariate scattergram (Figure 1).

Both sexes were compared across localities. Complete separation into the four original groups was not achieved after the 16 variables were tested, but six characters were significant and in descending order of best discrimination were KEEL, ULNA, FEML, MNDB, CRCD, SKLL (Table 3). The F-value for KEEL (25.28) is approximately 5 times as large as that of the next discriminator, ULNA, at 5.84. Inspection of classification cases after 16 cycles shows all German males correctly classified, three German females misclassified as Illinois males, six Illinois males misclassified as German females and one Illinois female misclassified as a German female (Table 3). Failure of specimens to be properly classified might be rectified by increasing the number of characters assessed. The best discriminators are three characters associated with flight, two with foraging and one with foraging and perching. It is also important to take note of the ordering of size of OTU's, which shows both that males are generally larger than females and that German males are larger than Illinois adults, but that there is no sharp distinction between German females and Illinois males (Figure 1).

TABLE 3: Best discriminators among 16 characters of 4 samples of *P. montanus* after 16 cycles of stepwise discriminant function analysis: Significant discriminators in descending order of magnitude of discriminating quality

Character	F to remove
Keel length	25.2829
Ulna length	5.8367
Femur length	3.9774
Mandible length	4.0569
Coracoid length	3.8588
Skull length	3.6317

Final classification after 16 cycles of SDFA

	German ♂♂	German ♀♀	Illinois ♂♂	Illinois ♀♀
German ♂ ♂	11	0	0	0
German ♀ ♀	0	9	3	0
Illinois ♂ ♂	0	6	23	0
Illinois ♀ ♀	0	1	0	13

Discussion

It seems clear from both the univariate and multivariate analyses that differences in size of bony variables have developed since the separation of the parental and imported stocks of *P. montanus.* In contrast with my earlier study (BARLOW, 1973) some variables of skin dimensions, including bill, tarsus and wing lengths, subject to differing environmental modalities, did not show significant differences in North America and yet another character, tail length, had changed significantly. Change in this latter character was postulated to have a genetic basis perhaps reflecting adaptation to a differing environmental abrasiveness in America. Now in the present study we see significant differences in some trophic apparatus variables between German males or both adults and Illinois females, which might relate to differences in diet between the two populations. Alternatively, as would be the case for all characters which vary significantly between the two populations, we may simply be seeing one manifestation of the development of a smaller bird in the New World.

A byproduct of the univariate and multivariate analyses was the demonstration of smaller size in characters associated with flight in the New World birds. The smaller size of KEEL in American *montanus* indicates a less massive development of flight muscles there where the birds are essentially sedentary with major flights being restricted to feeding forays and occasional interflock dispersal (BARLOW, 1973). In contrast, in Europe flight muscle size, as reflected by larger sternal characters there, may be associated with migratory or partially migratory habits of some European populations of *montanus.*

FEML, TBTR, and TRMT are multipurpose characters associated with perching, general terrestrial locomotion and specific terrestrial foraging. Again, small size in Illi-

nois females may simply reflect an inherent smallness or reveal emerging behavioral differences between New and Old World populations with respect to foraging and perching.

Jonston & Selander (1971) have found sexual dimorphism in size of characters of the flight assemblage between male and female *domesticus* which they attribute to the greater exigencies of fighting in males. The larger size of male *montanus* is likewise amenable to an explanation based on male-to-male aggressiveness, perhaps accentuated in this species wherein behavior may compensate for lack of plumage dimorphism between the sexes. This would be Darwinian sexual selection in *montanus* as previously implicated by Johnston (1973) for increased size of flight assembly characters in male *domesticus.* Johnston et al. (1972) further suggest that in this species enhancement of differences in the sizes of sexes may reflect response to winter climate. Although, as previously mentioned, bill size in *montanus* is slightly or significantly smaller in North American birds, at least when Illinois females are compared to German males, characters reflecting size do not differ significantly between the sexes. Thus, an interpretation of common diet between the sexes seems appropriate in this species as well.

If all differences seen between New and Old World populations of *montanus* are explicable on the basis of the genetic constraints of the founder principle (Mayr, 1963), as I postulated for skin characters (Barlow, 1973), then smaller size of New World birds is a concomittant of genetic isolation in America of a restricted subset of the total *montanus* genome available in Germany. We are seeing a gene pool molded in another environment (Germany), but selected for in America by adaptive modalities operative there. In view of the relatively small number of generations (1870—1977) upon which selection has had to operate it is not surprising that significant phenetic differences have not emerged between all skeletal characters compared. General absence of differentiation of phenotypic skin characters (except for tail length) and only partial elaboration of differences in skeletal characters suggest that *montanus* is still evolving in North America and that all of the genetic variability of the original innoculum, as small as it was at 20 birds, has not yet been realised. Johnston & Selander (1971) have similarly explained lack of complete differentiation in North American *domesticus.* Perhaps development of smaller birds in the New World may be attributable to genetic drift but limited evidence, at present, precludes elaboration of such an hypothesis.

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Has the Golden Sparrow replaced the Black-faced Dioch in West Africa ?

Gérard J. Morel and Marie-Yvonne Morel

Introduction

The balance between the Black-faced Dioch *(Quelea quelea)* and the Golden Sparrow *(Passer luteus)* has been severely altered during the last 25 years in the Lake Chad area and in West Africa. While *Quelea* was formerly the most abundant pest species, *P. luteus* is currently destroyed. Since it is claimed, especially in Nigeria, that *Quelea* has been reduced artificially, it has been suggested that the recent increase of *P. luteus* is the result of *Quelea's* eradication, these two species being potential competitors. As an alternative explanation, it is proposed (Jones, 1976; Copr, 1977) that the cyclical fluctuations of these avian populations are a response to climatic variations. The purpose of this paper is to discuss the first hypothesis — competition — through a comparison of both species.

Systematics and distribution

Passer luteus and *Quelea quelea* are both small passerines of the Ploceidae. *P. luteus* (Passerinae) is the most numerous and the most colonial sparrow in tropical Africa. It ranges over the Sahel from the Atlantic Ocean east to the Red Sea whence it enters South Arabia as the sub-species *euchlorus*. The genus *Quelea* (Ploceinae) has only 3 species restricted to the Ethiopian region. The nominal species *Quelea quelea* is by far the most important and we shall deal only with the West African sub-species *quelea* which ranges from the Atlantic coast to Lake Chad.

Plumage and moult

Quelea has a seasonal and sexual dimorphism but outside the breeding season, both sexes are identical. *P. luteus* has permanent sexual dimorphism and the only change in breeding dress is the black bill of the male.

In non-breeding dress, male and female *Quelea* have an identical plumage, which may help reduce aggressiveness and make social life easier (Wynne-Edwards, 1962). The Golden Sparrow presents an interesting denial to this hypothesis since the males keep their conspicious yellow plumage all the year round which does not appear to hinder their social life. The permanent "breeding dress" enables the sparrow to breed at any season and can be an opportunistic adaptation. The plumage of the Golden Sparrow is also noteworthy. It is the only sparrow to have such a rich dress and one cannot help but compare it with the plumage of the savanna weavers *(Ploceus)* which is also bright yellow.

The habitat

It extends, broken only by two rivers, from the Ocean to Lake Chad. It lies within the tropics, with an annual mean temperature of 29° C and rains of the monsoon type

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in summer. Despite an apparent monotony, the habitat heterogeneity is amazingly high, because the rainfalls are seasonal and of unpredictable importance (*P. luteus* ranges within the 100/500 mm isohyets; *Quelea* within the 200/1,200 mm isohyets) and because also the gentle relief and the soil diversity create conditions for a complex plant community (VALENZA & DIALLO, 1972).

They feed only on grass seeds which they hull. *Quelea,* at the start of the dry season, feeds on medium-sized and well concentrated seeds, easy to collect (especially *Panicum laetum* and *Echinochloa colona*). Then, as the dry season progresses, *Quelea* takes seeds smaller and smaller and more scattered: *Dactyloctenium aegyptium, Chloris* sp., *Schoenefeldia* (WARD, 1965).

The Golden Sparrow's diet is comparable to *Quelea's* but shows several pecularities: a very high percentage of *P. laetum* and a total absence of *Echinochloa* (MOREL & MOREL, unpubl.).

The crops *Sorghum* and *Pennisetum* are damaged by *Quelea* and the sparrow as well but rice is eaten only by *Quelea,* a remarkable difference. Besides, each species has its own feeding behaviour: *Quelea* forages in enormous flocks which accounts for the heavy losses it inflicts, especially on flood plains where the wild seed crop is abundant. *P. luteus,* which is more a desert bird, is better adapted to exploit a patchy or scattered food on grounds of lower productivity. This sparrow's ability to range up to the desert border and to exploit vast arid plains (e.g. the Ferlo south of the Senegal river) where *Quelea* is never found, is consistent with this statement.

Reproduction

Both species are colonial but, while the Golden Sparrow breeds in the dry season, *Quelea,* as a rule, breeds in the rainy season. The Golden Sparrow breeds only in the thorn-bush but *Quelea* can also breed on reeds in swamps and on sugar-cane. For convenience, we shall restrict this study to the colonies of the rainy season located in the thorn-bush.

Structure of the vegetation in a colony

It has been recently analysed in the Chad area by GASTON (1976), who recognized several conditions for *Quelea:* a) a percentage of tree cover of 20 to 50 %, where thorny trees 4 to 6 meters high are dominant and cover is also preferably regular; b) the grass layer (mainly Gramineae) is of variable height (30 to 200 cm) but with 100 % cover; c) the area is fairly humid, rarely saturated; d) there must be rich and open grass areas in the neighbourhood. Those conditions have also been met in Senegal and Mauretania.

The vegetational structure of the Golden Sparrow's colonies has only recently been given some attention. But it immediately looks different. The nests are built also on thorny trees, *Acacia* and *Balanites,* but their density per hectare is usually lower than for *Quelea.* Sometimes, both species breed alongside in the same area (e.g. in Mali; BORTOLI, 1977). The vegetation structure is a very important element of the habitat so it is likely that any serious alteration would cause changes in the bird distribution. Recently, the vegetation of this region has badly suffered from the drought (POUPON & BILLE, 1974). In many other places, the tree cover necessary for *Quelea* disappeared

almost completely through the combined action of man and climate. It is not too far-fetched to assume that *Quelea* may leave an area when the trees are getting scarce. If *Quelea* moved to the south because of the alteration of its habitat, among other things, it is unlikely it will make a come-back soon considering the time the woody vegetation needs to recover (Poupon, 1977).

The nest

The nests of these two species are strikingly different. *Quelea* builds a typical weaver's nest, an elongated sphere, made of long, green, supple grass. Unlike other weavers, *Quelea* does not add any lining to its nest. This loosely woven nest is however fairly strong and withstands the stormy rains very well. Several nests happen to be woven together indicating a very weak territoriality and obvious adaptation to colonial life. On the other hand, the nest by itself is a rather poor deterrent to predators (Morel & Bourlière, 1956).

The Golden Sparrow's nest is not comparable. It is an enormous sphere of thorny twigs with a cup of soft material. Indeed, it is unique among sparrows. But, really, it is just an adaptation of the domed nest. Cavities would never meet the demand of colonial nesting. Straw nests would collapse during the strong rains and would easily be torn open by any bird of prey of average size. It is well adapted to colonial life, to adverse weather and to predation. But its necessary positioning in thorny trees is a shortcoming.

Colonial breeding

Quelea and *P. luteus* are two colonial species, which breed during the rains in the same thorn-bush. But the similarity does not go farther. Both species are roughly subjected to the same environmental pressures but each species evolved its own response. In an unstable and unpredictable environment, a wise strategy seems to spread out the breeding season so that the hazards are divided. This is the Golden Sparrow's strategy. Conversely, the reproduction of large fractions of this population at the same time may produce disaster if the best breeding requirements are not met. *Quelea* has evolved just this second solution, but the timing and the synchronization of breeding are good and the fledging success is unusually high.

a) *Quelea*

The breeding season depends upon two closely related factors: a) green grass stalks. They are supple enough for weaving for a short period, so the birds have responded by synchronized and fast building. This clearly favours colonial behaviour. The grass is good for weaving after 200 mm rainfall, which occurs in the second half of the rainy season. b) food of nestlings. They are fed fresh grass seeds, still in a dough stage, and insects. It is not clear whether the time of breeding depends more on building material or the nestling's food, since the two factors are closely linked. Hatching occurs when the insect production is rather on the decline. In addition, the fresh seeds, which are given to the nestlings, produce less calories than fully mature seeds, which means consequently more visits and more distance for the parents to cover. And we have some evidence that the parents are already working near their limit (Ward, 1965 b). The

breeding must take place also when there is a maximum of rain ponds. Some do not last more than a few weeks and we know of several colonies in jeopardy for lack of water. *Quelea's* big colonies (hundreds of thousands of nests can be packed over a small surface) seem, after numerous observations, to be free of any significant predation. This remarkable condition is largely attributed to the size and short duration of the colonies. It has been called "the swamping effect", i.e., the size of the prey population is too big for any predator. Natural evidence for this hypothesis is given by the small colonies which suffered, in several instances, heavy destruction (THIOLLAY, 1975).

Clearly, the colonial reproduction of *Quelea* is the result of several intertwined factors which are very difficult to separate. Thus, *Quelea* copes successfully with an unstable environment thanks to fast and synchronized reproduction at the right time.

b) *Passer luteus*

The reproduction of the Golden Sparrow depends primarily upon the insects which are given to the young and to a lesser extent upon the twigs for the nests. These requirements differ strikingly from those necessary for *Quelea* (MOREL & MOREL, 1973; MOREL & MOREL, 1976). Though our knowledge of the production of insects is very crude, everyone agrees it is unpredictable and variable. It is still impossible to establish any logical relationship between rainfall and insect abundance let alone between the rainfall pattern and the sudden peak of one or several species. The peak of abundance of insects is sometimes fairly short, and some colonies, perhaps even fractions of colonies, must experience food shortage. Given these environmental constraints, we can understand why the Golden Sparrow colonies are unsynchronized. They are also very loose since the average number of nests per tree is no more than two (compare with *Quelea* figures). The scattering of the colonies is related to several possible factors: a) males' aggressiveness at the nest-building stage. Although this sparrow is a seed-eater most of the year, during the breeding season they behave like an insectivorous bird so that pairs need to be spaced out to get a sufficient amount of prey. Surprisingly, the crop (which is used during the dry season to store the seeds) is not utilized to carry the insects which are instead taken one by one. b) dispersion of the breeding population over large areas of suitable vegetation to adjust as closely as possible to local variations of food supply. c) the nest materials, though we lack positive evidence, could be a limiting factor. The nest is made of thorny twigs, of about 15 cm in length, picked under or near the trees. On the other hand, termites, which are numerous and very active, destroy any accumulation of dead wood under the trees. So, although actual figures are lacking, suitable twigs may sometimes be in limited supply.

The site of the colony can be occupied about two months, for the birds arrive gradually. The synchronization of the colony is not great. The Golden Sparrow's loose strategy has several drawbacks.

The Golden Sparrow's colonies thinly scattered over large areas, with conspicuous nests, for about two months should be an extraordinary bait for predators. But the nest is a formidable challenge for most of them. For snakes and monitors, the nest is defenseless and we actually found those animals in the nest; but the reptiles, although they surely feast upon the nestlings as much as they can, do not represent the same danger as birds of prey, especially migrants, which can come together in fairly big numbers.

The lack of a true synchronization also requires the Golden Sparrow males to watch constantly over their nest during the nest-building stage to drive away neighbours trying to steal nest material. Nest-building takes 10 days for the sparrow (as against 2—3 for *Quelea*) and this period is even longer since all the males did not begin together. The male must also guard against its neighbours attempting to copulate with its own female. Again, these efforts are mainly due to the loose synchronization. Conversely, *Quelea*, with its rapid and synchronized reproduction, has brought all these efforts to an absolute minimum.

Conclusion

This comparative study of two species has brought out the important differences which characterize each of them. Although they live more or less in sympatry and on comparable food, each species shows a definite preference for a particular environment and a more or less dry climate. It is also interesting to note how two species which belong to two distinct sub-families show at the same time convergence and divergence in their behaviour. We can thus conclude that the decline of the Dioch and the increase of the sparrow are primarily due to environmental variations, more precisely to deterioration of the habitat.

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Body Size of House Sparrows: Reproductive and Survival Correlates

Edward C. Murphy

Introduction

Several studies have documented the rapid geographic differentiation in body size of House Sparrows, *Passer domesticus,* since the species was first introduced to North America last century (e.g. Johnston & Selander, 1973a, b). Studies of physiological (e.g. Blem, 1973; Kendeigh, 1976), behavioral (Cink, 1977), and survival (e.g. Bumpus, 1899; Rising, 1972) correlates of body size have complemented the studies of phenetic variation and provided insight into the adaptive significance of body size.

Females of intermediate size and large males survived better than other size classes of the same sex both during a severe winter storm in Providence, Rhode Island (e.g. Bumpus, 1899; Johnston et al., 1972; O'Donald, 1973) and through a typical winter in Lawrence Kansas (Rising, 1972; Johnston & Selander, 1973a). In both instances intrasexual variance in body size decreased (see Lowther, 1976, 1977). Yet Selander & Johnston (1967) noted no geographic patterns in intralocality variance in body size for either sex: intralocality variance is as high in severe as in mild climates. Here I will examine maintenance of morphological variation at Calgary, Alberta, Canada which is near the northern limit of the species' range in North America.

Johnston & Selander (1973a) suggested winter reductions in body size variance are balanced by opposing selective pressures at other times of the year. I will first report on the relationship between morphology and reproductive output to test the hypothesis that differential fecundity of size classes balances the selective pressures of winter.

O'Donald (1973) contended that although severe storms occur only infrequently, they may impose much of the selection on body size. However, typical, non-cataclysmic, events must also influence size (Lowther, 1977). Perhaps interannual variation in winter severity at a locality constitutes sufficient heterogenity in selective pressures on body size to continually restore variability. I will analyze adult survivorship through a mild winter in Calgary to evaluate the hypothesis that such a winter imposes contrasting selective pressures on body size to those of severe storms or typical winters.

Methods and materials

During two years of a study of breeding ecology of House Sparrows near Calgary, Alberta, Canada, 51° 05′ N, 113° 52′ W, I trapped adults in mist nets and at nest boxes and color banded them for individual identification. Measurements taken on trapped birds were: wing length (primaries straightened) to the nearest 0.5 mm, tail, tarsus, and bill length as defined by Johnston (1969: 209) to the nearest 0.1 mm, and weight to the nearest 0.25 g. As tail length was difficult to measure consistently, the accuracy of the tail measurements is probably considerably less than implied by the precision of the calipers, the measuring instrument.

In the breeding season adults were observed at nest boxes and identified if already banded. Unbanded adults were trapped at nest boxes. Pinowski et al. (1973) noted that

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nest desertion is most likely if the parents, particularly the female, are trapped during egg stages of a breeding attempt. Therefore I trapped adults at nest boxes only during the nestling stage. To minimize disturbance to the nesting pair, I made only one attempt to trap the unbanded adult(s) during a breeding cycle. If unsuccessful, the trapping attempt lasted 20 min. at most.

Collection and preliminary processing of the reproductive data are described in detail elsewhere (Murphy, in press, a). Adults identified or trapped at a nest box during one nesting cycle, and seen there during a subsequent nesting attempt the same season, comprised the sample for analysis of reproduction—size relationships. I assumed that such adults remained at that nest box the entire season (see Summers-Smith, 1963: 45—47).

Correlations between all size and reproductive variables were computed. Each variable was analyzed for skewness and nonlinear relationships with variables in the other suite using the BMDP2R routine (Dixon, 1975). Relations between the two suites of variables were examined with canonical correlation analysis (Dixon, 1975: BMDP6M). I deleted weight from the suite of size variables in this and all other multivariate analyses, as it reflects condition as well as size (e.g. see Packard, 1967).

To test for differences in morphology of adults nesting in boxes and those breeding at other types of nest sites I used a discriminant function routine (Dixon, 1975: BMDP7M). To assess the possibility that assortative mating by morphology occurred I tested for relationships between male and female morphology with canonical correlation analysis (Dixon, 1975: BMDP6M).

If a banded adult used a nest box throughout 1975 and was not seen again in 1976 I assumed it died in the interim. This assumption depends on nest site fidelity. Resighting was virtually certain if an adult used any nest box in 1976 but relatively poor if it nested elsewhere in the study area. Consequently if nest site fidelity were low many birds assumed to be dead were probably still living. I have no data that critically test this assumption, which I've based on Summers-Smith's (1963: 45—47) findings in England. In the present study 19 of the 24 adults resighted at boxes in 1976 were at the same box as in 1975, suggesting, at least, that nest site fidelity was reasonably high. Using discriminant analysis (Dixon, 1975: BMDP7M) I tested for morphological differences between known survivors and those i.e., "non-survivors" I did not see again.

Possibly there were trade-offs between reproductive output and survival (e.g., review by Stearns, 1977) that somehow act to balance the selective pressures of winter. I used the number of eggs laid and number of young fledged as measures of reproductive output of females and only the latter as a measure of male reproductive output. A more sensitive measure of reproductive output would include weight of fledged young (see Murphy, in press, b). However, weight at fledging varied seasonally (ibid) and weights of fledglings were unknown for one or more broods at several nest boxes in the sample. Consequently I could not use this measure in the analyses. I compared reproductive output of survivors and "non-survivors" both univariately (Student's t-test) and multivariately (Hotelling's T 2).

Results

I assessed the possibility that differential fecundity of phenetic classes balances differential winter survival by analyses of (1) correlation between morphology and repro-

ductive output of box-nesting adults, (2) morphological differences of adults according to type of nest used, and (3) assortative mating by body size.

I first tested my assumption that trapping of adults at the nest during the nestling stage had no effect on the success of that attempt. I compared the number fledged from undisturbed attempts and from those breeding attempts during which one or both adults were trapped. Fledging success was equivalent (MURPHY, 1977: 152), indicating that trapping did not adversely affect success of the breeding attempt. Occasionally trapping possibly resulted in desertion of the nest site once the nesting attempt was completed. For example, nine of the 94 adults trapped at boxes in 1975 were no longer at the same box during subsequent breeding attempts that year. However, disappearance could be related to factors unrelated to trapping effects, e.g. mortality or completion of the season's nesting activities.

Correlations between adult morphological variables and reproductive variables are summarized in Table 1. Only female weight and egg weight were significantly corre-

TABLE 1: Correlations between body size and reproductive variables[1]

	Wing	Tail	Tarsus	Bill	Weight
A. Males, 1975 and 1976 combined (n = 46)					
ATTEMPTS	0.131	0.198	−0.075	−0.089	0.019
NEGGS	0.031	0.147	0.006	−0.023	0.019
NHATCH	0.088	0.260	−0.103	−0.288	0.119
NFLEDGE	0.117	0.114	0.027	−0.015	−0.042
SUMEGGWT	0.003	0.203	−0.056	−0.094	0.111
SUMFLYWT	0.111	−0.041	0.017	−0.013	0.148
CLSIZE	0.086	0.034	0.074	−0.004	0.085
HMIN	−0.071	0.121	−0.094	−0.204	0.010
FLYN	0.011	0.074	−0.026	0.015	−0.135
AVEGGWT	−0.095	0.038	−0.121	−0.019	0.149
AVEFLYWT	−0.009	−0.150	−0.222	−0.016	−0.007
B. Females, 1975 and 1976 combined (n = 52)					
ATTEMPTS	0.040	−0.204	−0.051	−0.054	0.110
NEGGS	0.149	−0.084	−0.008	−0.179	0.176
NHATCH	0.244	0.168	−0.051	−0.208	0.160
NFLEDGE	−0.023	−0.042	−0.137	−0.032	−0.133
SUMEGGWT	0.227	0.073	0.011	−0.043	0.338*
SUMFLYWT	−0.155	−0.145	−0.135	−0.107	−0.085
CLSIZE	0.289*	0.193	−0.114	−0.084	0.033
HMIN	0.208	0.345*	−0.043	−0.172	0.053
FLYN	−0.009	0.110	−0.127	0.011	−0.153
AVEGGWT	0.217	0.256	0.044	0.104	0.529*
AVEFLYWT	−0.033	0.161	−0.110	0.183	0.242
AVEFLYWG	−0.000	0.033	−0.107	0.106	−0.090

* $P < 0.05$, ** $P < 0.01$

[1] Codes for reproductive variables which summarized seasonal reproductive output are: ATTEMPTS—number of clutches initiated, NEGGS—total number of eggs laid, NHATCH—total number of eggs hatched, NFLEDGE—total number of young fledged, SUMEGGWT—total weight of all eggs laid, SUMFLYWT—total weight of fledged young, CLSIZE—average number of eggs per clutch, HMIN—average number of eggs hatched per clutch, FLYN—average number of young fledged per clutch, AVEGGWT—average egg weight, AVEFLYWT—average weight of fledglings.

lated in the same manner in both 1975 and 1976 (see MURPHY, 1977). When I treated each sex-year combination as a separate sample (ibid.), only seven of the remaining 218 correlations were significant ($P < 0.05$), about the number that would be expected if the null hypothesis of zero correlation were always true. No correlations between morphological variables and measures of fledging success were significant (see Table 1).

I also explored relationships between morphology and reproductive output using canonical correlation analysis. No correlations between the two suites of variables were significant in any sex-year sample (details in MURPHY, 1977). Thus, no differences in reproductive performance among box-nesting House Sparrows could be correlated with phenetic differences.

Attempts in nest boxes fledged significantly more young than did those in other types of nests (MURPHY, in preparation). Differential reproductive success of phenetic classes could occur if nest type and morphology were related. For each sex body size of adults mist netted during the breeding season but not seen at nest boxes was compared to that of adults at boxes. The former group consisted of adults which either did not breed or bred at non-box nest sites, e.g. in trees or buildings. No separation of the two male group means was possible using discriminant analysis ($D\ 2 = 0.161$, $F_{(4,159)} = 1.440$, $P = 0.223$). The means of the two female groups could be separated ($D\ 2 = 0.224$, $F_{(4,174)} = 2.463$, $P = 0.047$). However, only 54.7 % of the females could be classified into the correct group on the basis of morphology, while 50 % would be classified correctly by chance. Much of the separation of the two female groups was achieved by tail length differences ($t = 2.41$, $df = 177$, $P = 0.017$). Length of the wing, tarsus and bill were equivalent. Tail length was the most difficult measurement to make accurately on the live birds, and consequently the differences may simply reflect measurement inaccuracies. The results of the classification procedure of the discriminate analysis indicate that body size and nest type were not strongly related during the study period.

I used canonical correlation techniques to test for assortative mating by morphology. Results of the analysis (Table 2) provide no indication that preferential mate selection by body size occurred.

Two additional factors that might balance the effects of typical mid-latitudinal winters or severe storms are (1) reproduction and survivorship trade-offs, and (2) annual differences in selective regimes. As most adult mortality is probably winter-related in Calgary (see BEIMBORN, 1967) and I have insufficient data to examine reproduction and survivorship trade-offs during the breeding season, I will confine this analysis to the relationship between reproductive output and subsequent overwinter survival.

Although total weight of eggs and the number of young fledged were originally defined as measures of female reproductive output, no discrimination between survivors and nonsurvivors on the basis of egg weight was possible, i.e., the total weight of eggs laid in the season was equivalent in the two groups. Thus, the analysis is reduced to a univariate comparison to that for males. Survivors of both sexes produced fewer young than nonsurvivors, but the differences are insignificant (females: $t = 1.057$, $df = 26$, $P > 0.2$; males: $t = 1.179$, $df = 20$, $P > 0.2$).

Differential mortality of body classes of each sex over the 1975—1976 winter was studied by comparing morphology of adults sighted at boxes in 1975 and seen the following summer with that of adults not resighted in 1976. Loadings of all morphological

variables on the first discriminant axis were of similar magnitude and of the same sign. Thus, this axis represents overall size. Surviving males were somewhat smaller and surviving females somewhat larger than nonsurvivors of the same sex. These differences are insignificant (males: D 2 = 0.918, $F_{(4,50)} = 1.594$, P = 0.205; females: D 2 = 0.421, $F_{(4,50)} = 1.035$, P = 0.398) but do indicate that sexual dimorphism was reduced.

TABLE 2: Canonical correlation analysis of body size of breeding pairs

Correlations[1]	MWING	MTAIL	MTARSUS	MBILL	FWING	FTAIL	FTARSUS	FBILL
MWING	1.000							
MTAIL	0.351	1.000						
MTARSUS	0.340	−0.131	1.000					
MBILL	0.067	0.212	0.041	1.000				
FWING	0.057	0.066	−0.180	−0.361	1.000			
FTAIL	0.075	0.201	−0.113	−0.233	0.599	1.000		
FTARSUS	0.079	0.127	−0.082	0.277	0.086	0.106	1.000	
FBILL	0.231	0.203	0.032	0.387	−0.112	0.107	0.343	1.000

Eigenvalue	Canonical Correlation
0.31263	0.55913
0.09933	0.31517
0.03280	0.18110
0.01263	0.11239

Number of Eigenvalues	Bartlett's Test for Remaining Eigenvalues		
	χ^2	df	Significance
0	15.50	16	0.48806
1	4.44	9	0.87977
2	1.36	4	0.85134
3	0.38	1	0.54029
4	0.	0	1.00000

[1] All codes initialized by M are for males, those initialized by F are for females.

Discussion

The preceding analyses provide no indication that phenetic variation and reproductive output are related in Calgary. Variability in reproductive success probably does not balance the selective pressures of severe storms or typical winters.

Random mating with respect to morphology would regenerate morphological variability simply as a consequence of sexual reproduction. Character complexes coadapted to the previous winter would be disrupted; phenotypes no longer present in the parental population would have a finite probability of occurring in the next generation. Consequently, variation lost in winter would be partially restored in the next generation (see Fig. 1).

However, nonassortative mating cannot balance directional selection as it is only a randomizing influence on phenetic variation. Both during the severe storm in Providence and through the typical winter in Lawrence, sexual dimorphism increased (JOHN-

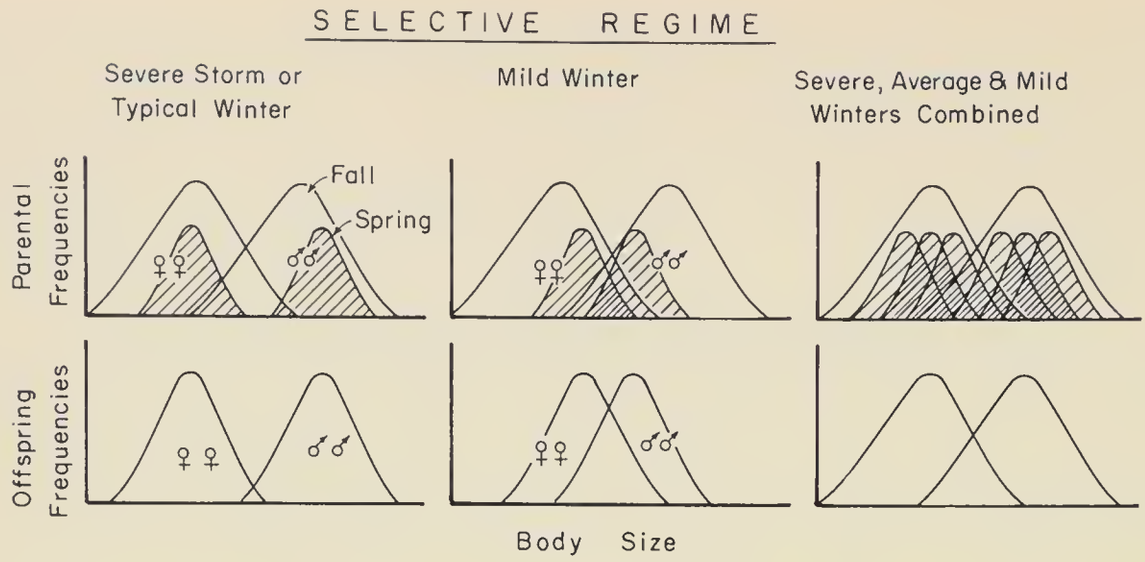

FIGURE 1. Temporal changes in morphological variation. Changes through average winters and severe storms depicted here follow patterns documented previously (e.g. JOHNSTON & SELANDER, 1973a). Pattern of change through the mild winter is drawn in accordance with results of the present study. Offspring variation is greater than parental variation in spring due to random mating (see text).

STON & SELANDER, 1973a). The 1975-6 winter in Calgary was exceptionally mild: January and February mean temperatures were 4.9 °C and 3.2 °C above normal, respectively. During that winter sexual dimorphism decreased, in contrast to the trends found in the Providence and Lawrence data. The optimum body size apparently varies from winter to winter. Interannual variability in winter selective regimes, as well as random mating, probably maintains intralocality size variation (Fig. 1).

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Comparison of Nestling Diets of Sparrows, *Passer* spp., Within and Between Habitats

Ted R. Anderson

Introduction

The principle of competitive exclusion, which states that two species competing for the same limiting resources cannot coexist indefinitely, is a widely held tenet of modern ecology. Very similar species commonly coexist in nature, however, and many studies have attempted to identify the means by which these species partition the resource environment and avoid exclusion of one or more species (recent reviews in Lack, 1971; Schoener, 1974; Colwell & Fuentes, 1975). These studies, usually of sympatric, congeneric pairs or sets of species, have frequently concluded that the species are either separated by habitat, or, if they are syntopic, by feeding station, by type or size of food utilized, or by temporal patterns of utilization.

An empirical generalization related to the separation of potential competitors by size of food utilized states that two congeneric species which forage for the same type of food in the same habitat differ in linear size of foraging apparatus by a factor of 1.3, larger to smaller (Hutchinson, 1959). Schoener (1965) modified this estimate downward to 1.14. The presumption is that this difference represents a partitioning of the food resource according to size, and that the observed difference represents the limiting similarity of one species to another which allows them to coexist (MacArthur & Levins, 1967). Lack (1971), for instance, makes this presumption 113 times in his review of ecological isolation in birds.

The House Sparrow *(Passer domesticus)* and its somewhat smaller congener, the European Tree Sparrow *(P. montanus),* are broadly sympatric in Europe and Asia, and were both introduced into the United States during the nineteenth century. The House Sparrow now has a wide distribution in North America and is sympatric with the Tree Sparrow in the latter's circumscribed range near Saint Louis, Missouri (its site of introduction). Comparative studies of the ecologies of the two species in their area sympatry showed that the two species breed syntopicly (in mixed colonies) and concurrently, and share nest site and nestling food niches (Anderson, 1978). The nestling diets of the two species showed a high overlap during the early part of the breeding season, but diverged considerably near the end of the season. This divergence coincided with increased rates of fledging success in both species.

The purpose of the present study was to test some hypotheses derived from the competition theory described above:

1. If the two species are using the same set of resources, the nestling diets of allopatric House Sparrow populations should resemble those of the Tree Sparrow populations more closely than do the diets of syntopic House Sparrow populations.
2. The House Sparrow should take larger items than the Tree Sparrow.

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Regarding the first hypothesis, the competitive exclusion principle predicts that divergence in resource use should occur between similar syntopic species, whereas the resource use of one species should expand in the absence of the second species. This logic is frequently used to explain the observed or presumed (due to increased bill length) expansion of resource use by island populations relative to adjacent mainland populations of the same species (i.e. CROWELL, 1962; GRANT, 1965). Regarding the second hypothesis, the culmen length of the somewhat larger House Sparrow is approximately 1.13 times larger than that of the Tree Sparrow (Fig. 1). This difference in length of foraging structure should result in a shift towards use of larger items by the House Sparrow.

Tree Sparrow House Sparrow

8.02 mm Culmen 9.09 mm

FIGURE 1. Culmen length of adult House Sparrows and Tree Sparrows (computed from data in RISING 1972 and BARLOW 1973).

Methods

In early spring 1976 nestboxes were put up in seven localities near Saint Louis, Missouri (Fig. 2). The four sites (B-E) near Portage des Sioux, Missouri are all in the region of sympatry between the House and Tree Sparrows. The three sites (F-H) in Monroe County, Illinois are inhabited by only the House Sparrow.

All sites were occupied farmsteads except site C, which consisted of the support buildings of a managed duck-hunting club, and site E, which was an unoccupied farmstead. Sites B-F were all located on the flood plain of the Mississippi River, while site G was situated just above the flood plain on the first terrace and site H was located in gently rolling hills 12 km from the river.

Nestboxes were checked at approximately weekly intervals from the beginning of April until synchronization of nesting was initiated. On 4 May the contents (eggs or young) were removed from all occupied nests at all study sites. Observations were subsequently made twice weekly to determine the dates of initiation of replacement clutches, their size and the approximate dates of hatching.

Food samples were obtained by the collar method (ORIANS, 1966). All items collected from all nestlings in a nest during 1 hr constituted a sample. Samples were refrigerated in ethanol at 4 °C until identified.

Food items were identified with the aid of a binocular microscope. Adult insects were identified to family (and occasionally to species) and each distinguishable species was assigned a number (e.g., Acrididae ad., sp. 1) and reference specimens maintained in ethanol for comparison with items identified later. Larval insects were identified to order (occasionally to family or species) and also assigned numbers (e.g., Coleoptera

lar., sp. 3). Arachnids were identified to order. Plant species were identified to species except for a few small seeds. The length of each item was measured to the nearest mm, and the volume of all items in a sample belonging to the same taxon was measured to the nearest 0.05 ml.

Comparisons between study sites and between species within a study site were based on summed data from all samples for a species from a site. A coefficient of overlap, C_λ, was computed according to the formula of Horn (1966), based on the volume proportions of the taxa in the diets of the two species from the same or different sites and from one species from different sites.

Figure 2. Map of the St. Louis region showing locations of the four study sites (B-E) in the region of sympatry between the House Sparrow and Tree Sparrow and the three study sites (F-H) outside the region of sympatry.

Results

Synchronization of the breeding activities of the two species was quite successful (Anderson, in press). Replacement clutches were initiated with a strong mode at 6 or 7 days after interrruption for both species.

A total of 299 samples from which 2742 items were identified were collected between 24 May and 8 June and the distribution as to species and study site varied from 4 to 125. The adequacy of the smaller samples to represent the nestling diet of the species at that site can be questioned. In an attempt to test the adequacy, a diversity index was computed for each species and site using the Shannon-Weiner formula. The values of the diversity index were then plotted against number of samples from a site in Fig. 3. Diversity values increase rapidly with number of samples for the sites with small numbers of samples but appear to peak with the sites having 17 samples, and show no consistent pattern thereafter. The relationship between number of samples and diversity can be adequately described by two straight lines (computed by the method of least

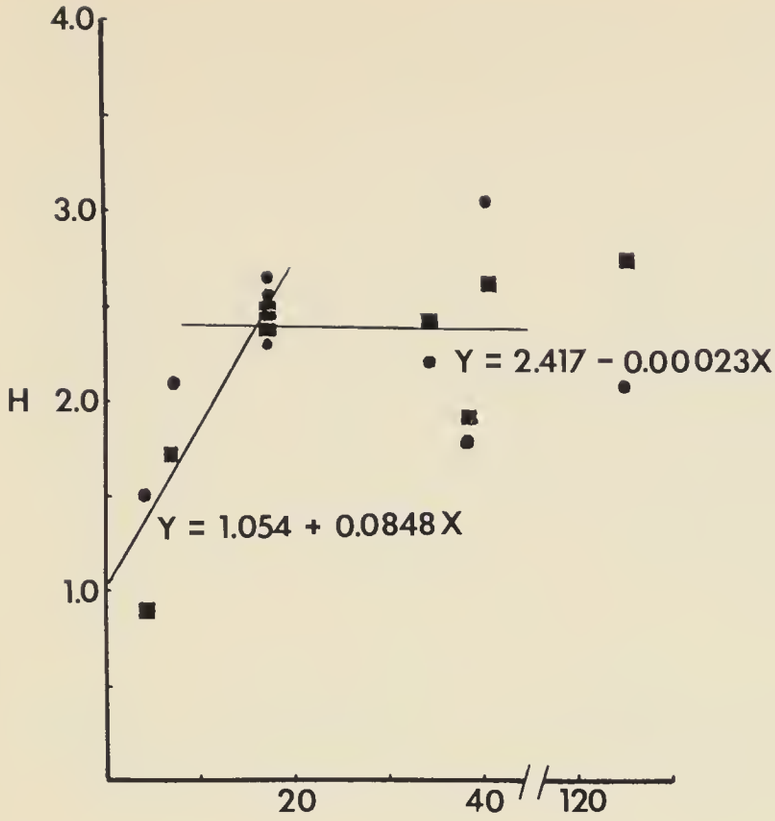

FIGURE 3. Graph plotting diversity indices (H) of nestling diets at a site (● volume proportions, ■ numerical proportions) against number of samples (abscissa) from the site.

squares; Fig. 3), and the intersection of the two lines is at 16, suggesting that 16 samples are capable of describing the diversity of the nestling diet of the two species.

In the analysis that follows the volume contributions of the various taxa are used because volume proportions more nearly represent the share of energy and nutrients provided by a particular taxon.

TABLE 1: Summary data on number of samples and items obtained per study site and on volume proportions according to kingdom at the study sites.

Species	study site	number of samples	number of items	volume % vegetable	volume % animal	volume % grit
House Sparrow (syntopic)	B	34	252	9.70	89.43	0.87
	C	7	168	1.47	98.53	—
	E	17	138	10.37	89.63	—
total syntopic		58	558	7.84	91.67	0.49
House Sparrow (allopatric)	F	40	442	8.63	91.17	0.20
	G	17	161	5.87	92.54	1.59
	H	125	967	9.32	89.19	1.49
total allopatric		182	1570	8.86	89.85	1.29
Tree Sparrow	B	38	330	9.66	90.00	0.34
	D	17	237	14.46	83.47	2.07
	E	4	47	10.53	89.47	—
total		59	614	11.78	87.14	1.08

Table 1 summarizes some of the basic data from the study sites and includes a breakdown of the diet according to kingdom. The plant materials consisted primarily of wheat *(Triticum* sp.), cracked corn, *(Zea mays),* mulberries *(Morus rubra)* and a few miscellaneous seeds, and comprised 1.5—14.5 % of the diet by volume. There are no consistent differences in the percentage of plant material between the syntopic and allopatric populations of the House Sparrow, or between House and Tree Sparrow populations. Grit, consisting of small stones, snail shells and fragments of chicken egg shells, made up a small fraction (0—2.1 %) of the diets. The large proportion (83.5—98.5 %) of the diets of both species consisted of animal material, entirely arthropods with the exception of a snail (Gastropoda) fed by a House Sparrow at one site. Both species regularly utilized spiders, but except for an extremely small number of mites and one phalangidid, the remainder of the diet consisted of insects. A complete list of the prey taxa and their proportions in the diets of the two species at the various study sites is available upon request.

TABLE 2: Coefficients of overlap, $\hat{C}_\lambda$, between study sites and between species for syntopic populations of the House Sparrow and Tree Sparrow and allopatric populations of the House Sparrow.

Species	study site	House Sparrow B	C	E	F	G	H	Tree Sparrow B	D	E
House Sparrow	B	1.0000	0.1072	0.3475	0.3624	0.7631	0.4152	**0.9623**	0.8401	0.4026
	C		1.0000	0.4764	0.1529	0.0561	0.0969	0.1485	0.2328	0.3209
	E			1.0000	0.5161	0.2351	0.1496	0.4351	0.7027	**0.7855**
	F				1.0000	0.3640	0.1762	0.3824	0.5443	0.4171
	G					1.0000	0.3375	0.7198	0.6374	0.1858
	H						1.0000	0.4069	0.3495	0.1390
Tree Sparrow	B							1.0000	0.8769	0.5061
	D								1.0000	0.7069
	E									1.0000

Coefficients of overlap were computed based on the volume proportion of each taxon (including plant, animal and grit material) in the diets of each species at each site. These coefficients are presented in Table 2. The coefficients are generally quite low between different House Sparrow populations, ranging from 0.0561 to 0.7631. The average coefficient of overlap between the allopatric populations (F—H) is 0.2926 ($s_{\bar{x}}$ = 0.0587), between syntopic populations (B, C and E), 0.3104 ($s_{\bar{x}}$ = 0.1082) and between allopatric and syntopic populations, 0.3053 ($s_{\bar{x}}$ = 0.0770). The coefficients of overlap between Tree Sparrow populations are considerably higher, 0.5061—0.8769 ($\bar{x}$ = 0.6966, $s_{\bar{x}}$ = 0.1072). The coefficients of overlap between the two syntopic populations of the two species were 0.7855 and 0.9623, the latter value more significant because of the small number of Tree Sparrow sample in the former (four samples from a single nest), while the latter represents the overlap for 34 samples of the House Sparrow and 38 samples of the Tree Sparrow at site B.

Table 3 presents data on the mean length and mean volume of items at each of the study sites. No pattern emerges, although mean item volume of syntopic House Sparrow populations was somewhat greater and mean length was less than in allopatric

TABLE 3. Mean item lengths and mean item volumes of food items from the various study sites.

Study site	B	C	D	E	total syntopic	F	G	H	total allopatric
House Sparrow									
mean length	9.8	5.8	—	5.8	7.6	5.7	6.4	7.6	6.9
($s_{\bar{x}}$) (mm)	(0.41)	(0.17)		(0.21)		(0.19)	(0.51)	(0.17)	
mean volume (ml)	0.046	0.028	—	0.029	0.036	0.022	0.037	0.047	0.039
Tree Sparrow									
mean length	8.4	—	7.3	5.9	7.8				
($s_{\bar{x}}$) (mm)	(0.30)		(0.29)	(0.37)					
mean volume (ml)	0.045	—	0.051	0.020	0.045				

populations. Mean length and volume of items from all Tree Sparrow populations were greater than in either allopatric or syntopic House Sparrow populations.

At site B, where large numbers of both species bred and a large number of samples were taken from both species, mean item volumes are essentially identical but mean item length is significantly greater in the House Sparrow ($t = 2.822$, $P < 0.01$). To examine this difference more closely, the mean lengths of items from the most important prey taxa were compared (Table 4). The six taxa made up a total of 74.1 % by volume of the House Sparrow samples and 87.4 % of the Tree Sparrow samples. When individual taxa are compared, there is no significant difference between the two species in the size of prey taken. The principal difference between the two species appears to be the result therefore of the larger number of *Hippodamia convergens* larvae in the Tree Sparrow samples than in the House Sparrow samples (165 vs. 66).

TABLE 4. Comparison of the mean lengths of items comprising more than 4 % of the diets of one or both of the species at site B.

	Tree Sparrow				House Sparrow			
	length (mm)			volume percent	length (mm)			volume percent
	n	$\bar{x}$	$s_{\bar{x}}$		n	$\bar{x}$	$s_{\bar{x}}$	
Wheat	15	7.8	0.47	8.2	15	6.9	0.21	9.1
Hippodamia convergens								
Larva	165	6.0	0.08	17.0	66	6.0	0.11	7.4
Pupa	13	6.5	0.18	2.0	24	6.7	0.17	4.8
Adult	18	6.6	0.18	6.8	8	6.5	0.19	2.2
Lepidoptera								
Larva Sp. 1	3	16.0	2.31	2.4	6	19.3	3.34	4.3
Noctuidae								
Pseudaletia unipuncta								
Larva	59	18.3	0.63	51.0	66	17.5	0.64	46.3
Total	273	8.9		87.4	185	10.7		74.1

Discussion

It is apparent that the results of this study do not conform to the hypotheses derived from competition theory. The two species showed no divergence in diet when they occurred syntopically; rather the coefficient of overlap between their nestling diets at the most thoroughly sampled site was close to unity. The diets of the allopatric House Sparrow populations differed markedly from those of syntopic House Sparrow and Tree Sparrow populations, and even differed markedly from colony to colony, apparently reflecting utilization of locally common prey items. Further, the two species took the same sizes of prey in the most commonly utilized prey taxa. It can be concluded that the two species used the same resources to feed their young when they occurred syntopically.

The fact that the two species take the same sizes of prey in spite of their different bill sizes raises questions about the conventional interpretation of the significance of bill size differences between closely related species. The presumption that species with different-sized bills take different-sized foods has been negated in other studies of related species when they are foraging in the same habitat (Pulliam & Enders, 1972; Abbott et al., 1977). The great differences observed between different populations of the same species feeding young of the same age at the same time suggests the importance of making within-habitat comparisons of resource use by potential competitors. Comparisons based on observations made over large geographical areas and over large time periods (i.e. Hespenheide, 1971) may not reflect the real pattern of resource use by the species when they are occupying the same habitat at the same time. MacArthur & Pianka (1966) provide a theoretical basis for explaining the high degree of overlap in the diets of two species (based on the cost of adding a particular item to the diet versus the expense of its addition) which begs the question of the role of competition.

This leads to the larger issue, an explanation of how the two species continue to coexist in spite of the fact that they are functioning essentially as a single ecological unit in exploiting the nestling food resources. Several alternatives to explain the results of this study will be briefly discussed: (i) food does not limit reproduction in these species, (ii) although food may be limiting reproduction, it is not "the limiting factor" controlling sparrow populations, and (iii) the House Sparrow-Tree Sparrow interaction is atypical because of their close association with man.

The fact that two or more species share a common resource does not necessarily imply that they are in competition. Common resource utilization is a necessary but not sufficient condition for competition (Birch, 1957). The shared resources must be limiting resources, operationally identified as those resources which, when reduced by increased numbers of a species or its potential competitor, result in an increased mortality rate or a reduced natality rate in the species (Anderson, 1978). The most widely held theory regarding the control of reproduction in altricial birds is Lack's hypothesis that it is food-limited (Klomp, 1970). This study did not address directly the question of whether food is, in fact, limiting reproduction. Evidence from earlier studies, however, including the inverse relationship between fledging success and nestling food overlap mentioned above, does suggest that food is a factor limiting reproduction in these species (Anderson, 1977, 1978).

It might be argued that the two species coexist in spite of competition for nestling

food because this resource is not "the limiting factor" controlling sparrow populations (cf. LACK, 1971). This is a specious argument, at least as it pertains to the study of most natural populations of plants or animals. Plant ecologists have devoted much research to the quest for "the limiting factor" of a particular species, with the general conclusion that factor interaction is so important and complex that identification of a single limiting factor is not possible (DAUBENMIRE, 1959). The insistence that there is a resource acting as "the limiting factor" for a species or set of species and that only competition for this resource results in competitive exclusion makes the principle untestable in the real world. One of the major difficulties is that it is impossible to operationally define "the limiting factor" of a population. ENRIGHT (1976) has recently shown theoretically how the interaction between density-dependent and density-independent factors can determine species distributions.

LACK (1971) suggests that species that are ecologically isolated in their primeval habitats may not be so isolated in man-altered habitats that they have recently begun to occupy. The House Sparrow and Tree Sparrow both reside in close association with man, and it could be argued that the overlap in their exploitation of nestling food may be the result of recent contact in the heavily man-altered environment. This argument does not apply effectively to these two species because the House Sparrow has probably evolved as a species in association with agricultural man in the Near East and Europe (JOHNSTON & KLITZ, 1977), and the Tree Sparrow may have a similar evolutionary history with agricultural man in the Far East. Their shared commensal relationship with man is therefore of long duration.

The competition for shared resources observed in these two species provides an excellent opportunity for the study of competition in free-living bird species. Much is known about the biology of these two species (see PINOWSKI & KENDEIGH, 1977), and many of their attributes make them ideal for experimental studies aimed at elucidating some of the difficult questions relating to the role of competition in determining bird distributions and community structure.

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SYMPOSIUM ON
CO-EVOLUTIONARY SYSTEMS IN BIRDS

9. VI. 1978

CONVENERS: D. W. SNOW AND W. J. BOCK

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Ecological and Evolutionary Aspects of Bird-Flower Coadaptations

F. Gary Stiles

Introduction

Until recently most of our general knowledge about the pollination of flowers by birds was summarized in the "syndrome of ornithophily" – that list of features adapting flowers for bird pollination, and the corresponding attributes of the birds (Faegri & van der Pijl, 1966). However, a glance at this syndrome shows that its compilers were much more interested in flowers than birds – or even than the plant as a whole. This narrow emphasis has broadened of late, as the study of pollination has moved into the mainstream of ecology. In particular, the wealth of recent studies on nectar-feeding birds and their flowers has changed many of our views regarding bird-flower coadaptations, and various features of the syndrome of ornithophily require reinterpretation. In this paper I attempt to present a balanced view of the coadaptations of birds and flowers, then proceed to a geographical survey of bird-flower coevolution.

Floral Adaptations to Bird Pollination

I distinguish three primary functions of the flower besides pollination itself: advertisement, reward, and filtering. Adaptations for advertisement draw the pollinator's attention to the flower, and are thus intimately related to its sensory perception. The reward (real or simulated) is related to the pollinator's energetic, nutritional, or sexual needs and provides the reason for visiting the flower. Filtering mechanisms restrict access to the reward to a particular subset of the available potential visitors, and may operate at the level of advertisement or reward by making the flower inconspicuous, or energetically expensive for some visitors.

In bird-pollinated flowers, advertisement is primarily by flower colour. The long controversy over whether nectarivorous birds prefer red (Grant & Grant, 1968) tended to obscure the fundamental importance of long-wavelength colours in general (Stiles, 1976) and the fact that different colour schemes represent advertisement strategies related to the ecology and phenology of the plant. For instance, in open habitats or dense plant populations the flowers themselves are often conspicuous, perhaps partly or wholly red. In dense vegetation or with scattered plants, a more long-lived signal may be advantageous: a large, colourful inflorescence, colourful leaves etc. The flowers themselves may then be short-lived, and inconspicuous except as they contrast with the main signal. Exposure of the flowers to destructive nectar thieves might thus be minimized, important for plants in habitats like tropical rainforest where such animals are numerous (e.g. *Heliconia;* Stiles, 1975).

Nectar is the chief floral reward to birds. Bird flowers generally show much higher nectar volumes than do insect flowers (Cruden et al., 1978); in the wild, nectar volume is a prime determinant of flower choice by birds (Hainsworth & Wolf, 1976; Stiles, 1976).

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Bird-flower nectars are rather dilute (Baker, 1975) and generelly low in amino acids (Baker, 1975). Of the three main sugars present sucrose predominates in nectars of hummingbird flowers, glucose and fructose in those of flowers pollinated by perching birds (Stiles, 1976; Baker & Baker, 1978).

Pollination itself is most meaningfully understood in terms of the genetic structure and breeding system of the plant population; whether facultatively or obligately self- or cross-pollinated. This will determine the optimal pattern of pollen movement; the foraging patterns and social systems of the available pollinators will in turn determine which of them is the optimum pollen vector. The floral reward should be rich enough to encourage revisitation, but poor enough that the pollinator must move between an appropriate numbers of flowers to satisfy its requirements. The amount and sugar content of the nectar offered by a flower or plant can be adjusted, through natural selection, to the prevalent dispersion of the plant population and the energetics of foraging behaviour of the pollinator, so as to optimize pollen flow. Different pollinators may employ different foraging strategies, according to the spatial dispersion of flowers. Dense concentrations of flowers facilitate territoriality, which can reduce pollen movement to and from the defended flowers, but increase reliability of visitation (Linhart, 1973; Stiles, 1978, 1978a). Scattered flowers favour a traplining mode of visitation, maximizing cross pollination but reducing reliability and fidelity of the pollinators (Stiles, 1978a). Large pollinators and/or scattered plants favour production of more, or more concentrated, nectar (Heinrich & Raven, 1972). The amount of reward per plant (or clone) can be adjusted by varying the rate or synchrony of inflorescence and/or flower production, as in the different species of *Heliconia* (Stiles, 1975).

Producing large amounts of nectar per flower has several consequences for the plant. Nectar flow is directly correlated with flower weight, reflecting mainly the increase in protective tissues of nectar-rich flowers (Opler, 1978). This tissue protects nectar and sexual organs of the flower principally against attacks by destructive nectar thieves, rather than against the "hard beaks" of pollinating birds (Stiles, 1978a). Bird pollination is thus doubly expensive to the plant on a per-flower basis, and will probably evolve only when this extra expense is more than compensated by enhanced pollination. Elsewhere (Stiles, 1978a) I discuss the ecological contexts in which birds can be optimal pollinators.

Filtering of the potential visitor spectrum operates at two levels: reducing visitation by non-birds (especially insects), and limiting the number of bird species to visit. Adaptations for the former include red coloration (to which bees are insentive), lack of corolla lip, free-hanging corolla, etc. (Faegri & van der Pijl, 1966; Raven, 1972). The latter mechanisms, no less important for reliable pollination, operate by differentially affecting the energetic efficiency of nectar extraction by birds whose beaks "fit" the corolla tube differently (Wolf et al., 1972); this can affect the birds' flower preferences (Stiles, 1978a).

In this connection, there are two principal types of bird-flowers: tube and brush. In the former the perianth forms a more or less lengthy tube that the bird's bill must traverse to reach the nectar. Brush flowers secrete nectar into a cup or shallow tube; the "brush" is formed by numerous stamens extending out in front of the cup. The bill-corolla "fit" is much more important in exploiting tubular flowers: the bill must be the right length and curvature, and must often be precisely oriented to reach the nectar; this can permit placement of pollen on a specific part of the bird. Brush flowers are much less effective as

filters: the nectar is usually accessible to a variety of birds, who become liberally dusted with pollen when visiting. Tube and brush flowers could thus differ greatly in their potentials for entering into exclusive coevolutionary relationships with pollinating birds, which in turn could affect the organization of bird-flower communities (see below).

Specializations of Flower-Visiting Birds

The classical "syndrome of ornithophily" does not distinguish between definite specializations for flower visitation, and attributes of birds in general. This distinction is necessary for evaluating coevolution of birds with flowers, and comparisons of different flower-bird groups in this respect. To this end I shall construct a hypothetical highly specialized flower-bird, then compare existing species and groups with this construct. The list of pertinent specializations might read as follows:

Size: small to very small; nectar per flower usually 100 μl or less. Small birds operate better at tips of twigs where many flowers are, require relatively less energy (above maintenance levels) for hovering; can also take smaller (thus more numerous) insects, satisfy protein needs more quickly and easily than large birds, allowing greater energetic dependence upon flower nectar.

Bill: long and slender for "legitimate" flower visits, or sharp and/or hooked for nectar robbing. The most highly coevolved types have bills closely corresponding in shape to specific flowers they pollinate.

Tongue: more or less tubular or grooved, and/or brushtipped, to facilitate capillary uptake of nectar (Hainsworth, 1973); capable of extension beyond bill tip.

Locomotion: agility, either in flight (hovering) or acrobatic abilities when perched; specialized flight apparatus or relatively large, strong feet.

Behaviour: aggressive behaviour and/or territoriality at flowers well developed (stationary, conspicuous, often defensible resource); highly developed spatial memory for systematic flower visitation, including traplining (comparative data on this point are lacking).

Annual cycle: breeding, moult and/or population movements synchronized with flower availability; dependence upon energy from flowers for successful reproduction or moult a more highly coevolved condition then "blossom nomadism" of nonbreeding birds.

By these criteria we can distinguish different degrees of specialization among the major groups of flower-visiting birds, as follows:

Trochilidae (hummingbirds): most species very highly specialized by all criteria (Skutch, 1975; Stiles, 1973, 1975; Snow & Snow, 1972).

Nectariniidae (sunbirds): many species approach hummingbirds in specialization; less specialized locomotion; less differentiation of bill types and fewer specific flower-pollinator relationships (Skead, 1976; Wolf & Wolf, 1976).

Meliphagidae (honeyeaters): some highly specialized (e.g. *Promerops;* Broekhuysen, 1959), but most depend on insects rather than flowers for breeding, tend to show low flower specificity and few tight morphological coadaptations; often rather large size (Officer, 1964; Keast, 1968; Carpenter, 1978).

Drepanididae (Hawaiian honeycreepers): some species quite specialized in behaviour and morphology; degree of flower specificity and dependence through annual cycle requires study (Carpenter, 1976, 1978).

Dicaeidae (flowerpeckers): a tight coevolutionary relationship of many species with mistletoes apparently involves greater specialization for frugivory than flower visiting (Docters van Leeuwen, 1954).

Loriinae (Lories): major specialization is papillate tongue, for taking pollen not nectar; otherwise differ little from most parrots in morphology and behaviour; mostly eat and destroy flowers; low flower specificity (Churchill & Christensen, 1970; Forshaw, 1973).

Coerebidae (honeycreepers): most species rather generalized; most specialized nectarivores *(Coereba, Diglossa)* primarily nectar robbers (Biaggi, 1955; Skutch, 1962).

Zosteropidae (white-eyes), Icteridae (American orioles and blackbirds): most species generalized, a few show slight to moderate specialization for nectarivory, may form coevolutionary relationships (Gill, 1971; Beecher, 1951; Cruden & Toledo, 1977).

In addition, I lack data on several small groups containing more or less specialized nectarivores: Irenidae, Callaeidae *(Philesturnus)*, Phileppittidae *(Neodrepanis)*. A larger number of more or less generalized passerine families contain species reported to visit flowers frequently: Sturnidae, Dicruridae, Pycnonotidae, Thraupidae, Parulidae, etc. These will not be considered further in the present context because their flower visitation is apparently mostly opportunistic, involving little or nor specialization. However, note that some plants (usually trees) have "cornucopia" flowers apparently adapted for attracting various more or less unspecialized visitors – with, probably, a resulting low percentage of fruit set (Gentry, 1974; Toledo, 1977).

Geography and Evolution of Bird-Flower Coadaptations

Most of the major groups of flower-birds are largely or entirely confined to a single zoogeographic region, suggesting that nectar-feeding – and bird pollination – have arisen independently several times. The Neotropical region shares no groups with the Old World; the Meliphagidae (except the possibly unrelated *Promerops*) and Loriinae are essentially confined to Australasia. The Ethiopian and Oriental regions share many groups, but most of the specialized sunbirds are confined to the former. Nectar-feeding is moreover a tropical phenomenon: the few Nearctic flower-birds were clearly derived relatively recently from the Neotropical, while the Palaearctic is essentially without avian nectarivores. This perhaps reflects the fact that high nectar production by plants is energetically most feasible in warm, moist climates (Huber, 1955; cf. Stiles, 1978a).

The Neotropical region contains the largest and most specialized assemblage of flower-birds, with over 300 species of hummingbirds alone. In terms of specialization, the Ethiopian with its wealth of sunbirds (and *Promerops*) comes next. The Oriental region contains rather fewer flower-birds, with a smaller nucleus of specialized types. Many species of flower-birds inhabit Australasia, but the degree of specialization for, and dependence upon, flowers seems rather lower overall than in other regions. Significantly in regions like the Neotropical and Ethiopian with many highly specialized nectarivores, tubular bird-flowers predominate; in Australia, nearly all native bird-flowers are the brush type (Skead, 1967; Officer, 1964).

These differences may in part reflect the different growth habits and taxonomic affinities of bird-flowers in different regions. The Neotropical and Australian regions offer an interesting contrast in this respect. Neotropical bird flowers are predominantly large succulent herbs (e.g. *Heliconia*), shrubs (many dicot families) and epiphytes (Bromeliaceae, Ericaceae, etc.) occurring at forest edges or light gaps, or in the canoppy (Stiles, 1978b). Most Australian bird-flowers are trees and shrubs of a single family, the Myrtaceae (e.g. *Eucalyptus*) characterized by brush-flowers, and often the dominant woody vegetation of a region (Keast, 1968). In the predominantly dry climate epiphytes and large herbs are few; the net result of these factors is a much less ecologically diverse assemblage of bird-flowers (cf. Officer, 1964). Conversely, the degree of dependence upon birds as pollinators in this region may previously have been overrated (Carpenter, 1978).

Communities of nectarivorous birds may also be organized along rather different lines in these regions. Many Neotropical communities contain 10 to 20 species of hummingbirds, plus several species of honeycreepers, icterids, etc. (e.g. Slud, 1960; Feinsinger, 1976). This richness results from various more or less specific plant-pollinator relationships, along with differences in foraging strategies, seasonal movements, habitat preferences, and dominance relations among the birds (Stiles, 1975; Feinsinger, 1976). Fewer nectarivore species seem to occur in a given Australian community, with much overlap in flowers used, few exclusive plant-pollinator relationships, often interspecific flocking and less territoriality. A major part of the diets of all bird species does not come from flowers; nectar is a less essential resource (Carpenter, 1978). These conclusions are still highly tentative; in-depth studies of natural communities of nectar-feeding birds and their flowers promise to be a fruitful field of inquiry in the next few years. Comparisons of these communities can illuminate not only bird-flower coadaptations, but also many aspects of biological communities in general.

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Fruit-Frugivore Interactions in a South African Coastal Dune Forest

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Introduction

Birds vary widely in the extent to which they are dependent on fruit for their energy and nutrient requirements, and in their degree of specialization to a frugivorous diet (Morton, 1973; McKey, 1975). Plants too differ in the number, size and quality of fruits that they produce (Janzen, 1969; Snow, 1971). The diversity may partly reflect differences in the processes and patterns of coevolution between plants and their dispersal agents (McKey, 1975; Howe & Estabrook, 1977).

This paper summarises current research into the nature and extent of fruit-frugivore interactions in a subtropical African coastal forest, with the aim of determining some of the coevolutionary relationships between plants and their avian dispersal agents. The data are relevant to testing predictions that: (1) plants relying on dependent and efficient specialized frugivores should produce limited numbers of high quality protein- and lipid-rich fruits, and (2) plants dispersed by a wide variety of mainly opportunist frugivores should produce many relatively low quality, carbohydrate- and water-rich fruits (McKey, 1975).

Study area and methods

Research was conducted from March 1977 to March 1978 in an evergreen coastal dune forest on the farm 'Twinstreams' near Mtunzini (28°58' S, 31°46' E), South Africa. The climate is subtropical with an average annual rainfall of 1204.5 mm. A dry season, with less than 100 mm rain a month, extends from April to September. Rainfall during the study period was 1331 mm.

A detailed account of the study area and vegetation is given by Moll (1972). A total of 117 tree species has been recorded for the farm (I. F. Garland, pers. comm.), 86 of which produce fleshy fruits. I have recorded 103 non-predatory bird species in the forest and surrounding habitats) 35 of which have been recorded eating fruit.

I made intensive observations over 675 hrs at fruiting individuals of 25 tree species and one mistletoe (Loranthaceae), *Erianthemum dregei* (Eckl. & Zeyh.) van Tieghem (nomenclature for the tree species follows Coates Palgrave, 1977). The data presented here derive from 482 hrs observation on 15 of the tree species and the mistletoe. Data for the other tree species will be referred to in general terms only, since I do not have chemical analyses of their fruits.

The spectrum of frugivores exploiting different fruit crops was monitored during peak fruiting periods at individuals with average or above average fruit crops. I chose trees at which the crowns were fully visible so that few, if any, visits are likely to have gone unrecorded. The duration of each visit was recorded to the nearest 0.5 s. I measured feeding rates where possible by noting the number of fruits ingested during a period of continuous timed observation. Since the objec of this was to estimate the number of seeds ingested per unit time, I ignored occasions when a species ingested pulp but not seed.

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Fruits for analysis were collected fresh and oven dried to constant mass. Analyses were carried out by the National Food Research Institute of the South African Council for Scientific and Industrial Research using standard techniques for the determination of lipids, protein (total nitrogen x 6.25), fibre and ash. Carbohydrates were determined by subtraction. The energy content of the flesh was measured by bomb calorimetry and the values expressed in kJ/ash-free dry gram. Fruit crop sizes were estimated by stratified sampling.

Results and Discussion

Four of the 35 bird species feed almost exclusively on fruit though *Tauraco porphyreolophus* and *Colius striatus* also eat foliage. Only *T. porphyreolophus* is resident in the forest. *Columba arquatrix* and *Treron australis* are subject to local movement in response to the ripening of certain fruit crops, while *C. striatus* is common along the edge of swamp forest, in heavily disturbed habitats and in gardens. Only 6% of the 6162 records of fruit feeding obtained during this study are attributable to this group.

Fruit is the main dietary item of eight other species: a hornbill *Bycanistes bucinator,* a starling *Lamprocolius corruscus,* three barbets *Pogoniulus bilineatus, P. pusillus* and *Buccanodon leucotis,* and three bulbuls *Pycnonotus barbatus, Andropadus importunus* and *Chlorocichla flaviventris.* Only *P. pusillus* is non-resident and uncommon. These are the most frequently recorded species at fruiting trees and 83% of all fruit-feeding records are attributable to this group.

The remaining 23 species feed predominantly on items other than fruit and account for only 11% of all fruit-feeding records. The most important species is the white-eye *Zosterops pallidus* to which about half of the feeding records of the group refer.

Nine species made over 90% of all visits recorded at fruit crops during periods of intensive observation (Table 1). The most frequent visitors were *C. flaviventris* and *P. bilineatus,* which are also the most abundant frugivores in the forest. The number (N) and diversity (H) of species recorded at fruiting trees were both negatively correlated with the wet mass of the seeds of these plants ($N = 12.2 - 21.4$ mass (g), $r^2 = 0.797$, $p < 0.001$, $n = 22$; $H = 1.9 - 2.6$ mass (g), $r^2 = 0.590$, $p < 0.001$, $n = 22$). The total number of species recorded at some of these fruit crops is slightly higher than the figures given in Table 1, which represent only the number of species recorded during timed observation periods. A total of 20 species have been recorded eating fruits of *Trema orientalis* (Ulmaceae), 18 at *Apodytes dimidiata* (Icacinaceae), 17 at *Halleria lucida* (Scrophulariaceae) and 16 at *Ficus natalensis* (Moraceae).

Visiting rates varied with time of day, being highest during the early and mid-morning hours. Average visiting rates varied from 54 visits/hr at *Ficus vogelii* to 0.6 visits/hr at *Strelitzia nicholai* (Strelitziaceae), though the majority of species received between 2 and 13 visits/hr.

Quantity and quality are important parameters of any seed dispersal system. The quantity of seeds dispersed by a species is a function of the visitation rate, the duration of visits and the rate of seed ingestion. The proportion of fruits (and hence seeds) ingested by different frugivores can be calculated (Table 1). *Pogoniulus bilineatus, C. flaviventris* and *T. porphyreolophus* are the most important consumers, with *P. bilineatus* ingesting the

greater proportion of small-seeded fruits, *C. flaviventris* taking mostly medium-sized fruits and *T. porphyreolophus* many of the large-seeded fruits. Each of the other species was an important consumer of fruits from at least one of the tree species studied. The number of fruits removed per hour (I) correlated significantly with the number of visits per hour (V) according to the function $I = 3.89\ (1.34)^V$; ($R^2 = 0.792$, $p < 0.001$, $n = 19$).

The quantity of seeds dispersed is important to plants colonizing temporally and spatially unpredictable germination sites. Such plants usually have large seed crops. McKEY (1975) argues that the general shortage of dispersal agents may be relieved by the evolution of fruits that are exploitable by a wide variety of frugivores, many of which will be opportunists. Such fruits will generally be rich in carbohydrates. The greater number of seeds taken from trees producing large crops of small-seeded carbohydrate-rich fruits (*Ficus and Halleria*) by a greater number and variety of frugivores than recorded at other trees (TABLES 1, 2), support this argument. (Analyses of *Halleria* fruit are not complete but the fruit is watery and sweet, which suggests a high carbohydrate content).

Fruit quality varied considerably between species (Table 2). Most fruits had high carbohydrate and low lipid and protein levels, while a few contained considerable lipid and moderate protein and carbohydrate levels. *Ekebergia capensis* (Meliaceae) fruits contained considerable amounts of protein. There was no relationship between the seed size and the quality of these fruits.

High quality fruits are considered to be the product of selection for maintaining the services of specialized dispersal agents (McKEY, 1975). According to this view, those species with high quality fruits listed in Table 2 should have special dispersal requirements which should be met by at least some of the species exploiting the fruits. Selection may favour an improvement in (1) the rate of removal of seeds after maturation, (2) dispersal agent reliability, (3) the probability of a dispersed seed reaching a suitable germination site intact, and (4) the distance that a seed is dispersed from the parent plant.

Strelitzia nicholai is a mid-successional species of secondary succession in forests which produces a limited number of large-seeded fruits with tufted fibrous arils containing very high proportions of lipids. Fruits are produced sparingly throughout the year, and are fed on by only three species. Both *P. bilineatus* and *B. leucotis* ingest and subsequently regurgitate seeds, which probably entails quality dispersal. The third species, *P. barbatus*, seldom ingests seeds.

Ekebergia capensis and *Trichilia emetica* (Meliaceae) are trees of mature forest. Both produce relatively large-seeded fruits which ripen asynchronously over an 11–14 week fruiting season. Dispersal of these seeds necessitates regular visits from frugivores capable of ingesting large seeds and confining dispersal to forest habitats. Specialized frugivores such as *T. porphyreolophus, B. bucinator, L. corruscus* and *P. bilineatus* will ingest and subsequently regurgitate large seeds and so probably meet these requirements.

Trema orientalis, Apodytes dimidiata and *Vepris undulata* (Rutaceae) are interesting since they have high quality fruits associated with small seeds. The spectrum of species exploiting these fruits is wide and includes a number of opportunists and less specialized frugivores. *Trema* colonizes disturbed areas in forest and fruits for about seven months of the year. A long fruiting season and constant rate of seed dispersal may favour the rapid dissemination of seeds to temporally and spatially unpredictable germination sites. The high quality fruits may be adapted to maintaining the services of potential dispersal agents

TABLE 1: Percentages of visits made and fruits taken by some frugivorous birds from various dune forest trees

	bird species[1]											visits[2] fruits	hrs obs.	H[3]	fruit crop size[4]
	Tp	Bb	Bl	Pb	Pl	Cf	Ai	Lc	Zp	OTH	TOT				
Halleria lucida			5	17	9	10		6	5	48	13	13	20	2.63	12
						no data									
Ficus natalensis	7	2	6	46	10	10		3	11	5	11	12	21	1.78	29
	54	9	2	19	4	7		1	2	2		62			
Ficus vogelii	1	16	24	8	14	25	1	2	6	3	12	54	20	1.91	32
						no data									
Trema orientalis				42	6	4	2	2	24	20	15	11	20	1.82	900
				64	2	1	1	2	23	7		242			
Antidesma venosum	2		4	41	13	5	1		21	13	11	3	29	1.80	79
	12		2	56	13	3	1		12	1		35			
Bridelia micrantha	4		4	2	38	41	4	1	2	4	12	12	25	1.44	84
	8		4	2	36	44	2	1	1	2		116			
Vepris undulata				38		29	16		8	7	11	6	27	1.63	20
				37		34	14		8	7		29			
Apodytes dimidiata				12	1	65	2	8	4	8	10	11	23	1.27	25
				6	1	68	1	21	1	2		80			
Sideroxylon inerme	2		2	20		59	13	1		3	7	5	38	1.21	35
	13		2	15		57	10	2		1		26			
Euclea natalensis	3		8	26	8	49	2			4	7	3	35	1.42	17
	11		4	18	9	53	4			1		11			
Mimusops caffra	19			12	12	44		13			5	2	12	1.45	3
	49			5	7	26		13				5			
Strelitzia nicholai			12	24	64						3	0.6	66	0.88	0.6
						no data									
Trichilia emetica	1	1		24	6	49	2	17			7	5	34	1.33	7
	1	3		24	2	43	1	26				28			
Dovyalis longispina	4		1	14	29	29	14	6	3		8	5	39	1.72	19
	34		2	10	21	16	9	8	0			7			
Ekebergia capensis	19	14	20	7	2	10	2	17	9		9	3	23	2.00	0.9
	38	33	11	1	1	4	1	11	0			8			
Erianthemum dregei				94						6	2	3	50	0.23	2.0
				95						5		14			

Table 1, continued

[1] Bird species: Tp, *Tauraco porphyreolophus;* Bb, *Bycanistes bucinator;* Bl, *Buccanodon leucotis;* Pb, *Pogoniulus bilineatus;* Pl, *Pycnonotus barbatus;* Cf, *Chlorocichla flaviventris;* Ai, *Andropadus importunus;* Lc, *Lamprocolius corruscus;* Zp, *Zosterops pallidus;* OTH, other species; TOT, number of species recorded during observation periods. For each species the given data represent the percentage of the visits made by a species, and (below, underlined) the percentage of fruits removed by that species

[2] Mean number of visits/hr and (below, underlined) mean number of fruits removed/hr

[3] Diversity $H = -\Sigma\, p_i \log_e p_i$, where p_i is the proportion of visits made by species i

[4] Fruit crop size of observed trees (x 1000 fruits)

Table 2: Composition of some dune forest fruits

	wet mass of seeds (mg)	wet mass of flesh (mg)	water (%)	pericarp constituents (as a % of dry mass)					energy content of flesh (kJ/AFDG)
				lipid	protein	CHO	fibre	ash	
Strelitzia nicholai	322	72	3.3	67.0	3.6	10.8	18.1	0.5	32.84
Trema orientalis	5	16	62.5	47.6	15.0	20.6	6.9	9.9	30.14
Trichilia emetica	384	540	57.6	46.9	8.5	31.1	10.4	3.1	28.65
Apodytes dimidiata	106	189	78.3	35.5	12.0	36.8	7.4	8.3	26.77
Vepris undulata	88 [1]	113	59.3	18.4	11.5	51.4	12.3	6.4	22.41
Ekebergia capensis	410 [1]	1444	74.6	8.6	21.6	53.7	9.8	6.3	20.72
Sideroxylon inerme	193	321	70.7	5.8	5.8	79.3	4.4	4.7	20.64
Ficus vogelii	3 [2]	4013	84.8	3.3	4.6	62.5	21.7	7.9	18.29
Mimusops caffra	307	1487	64.8	2.0	2.8	84.6	6.3	4.3	17.83
Dovyalis longispina	400 [3]	2841	87.5	0.8	4.8	87.2	4.0	3.2	17.58
Euclea natalensis	231	683	70.3	0.7	2.3	90.9	2.4	3.7	17.46
Bridelia micrantha	61	150	84.2	0.6	5.1	82.3	10.1	1.9	17.65
Antidesma venosum	36	100	78.0						17.24
Ficus natalensis	2 [2]	893	86.0						17.16

[1] total seed mass. Each fruit contains four seeds

[2] mass of a single seed. Each syconium contains approximately 400 seeds

[3] total seed mass. Each fruit contains two seeds

throughout the long fruiting season. The selective advantage of high quality fruits in *Apodytes* and *Vepris* is not clear.

Plants occurring on limited specialized habitats should have well developed adaptations that ensure high quality seed dispersal. Mistletoes (Loranthaceae) in particular appear to have special dispersal requirements in the form of dispersal agents capable of depositing the soft sticky seeds intact.

Erianthemum dregei is the common mistletoe of the forest. The fruits are dispersed only by the tinker-barbets *P. bilineatus* and *P. pusillus*. Though the majority of seeds are taken by *P. bilineatus*, both have a number of features which enhance their effectiveness as dispersal agents of the parasite. These include (1) rapid response to the appearance of ripe fruits, (2) considerable fidelity to individual clumps, and (3) regurgitation of seeds in a viable state. Regurgitated seeds retained their adhesiveness and germinated within 24 hours, the same time as required by experimentally deposited seeds. In return the birds are assured of a predictable food source. *Erianthemum* fruits consist of a thin oily aril around the seed and the fruits ripen asynchronously during two extended fruiting seasons in the year.

Fruiting takes place throughout the year in the forest, with a distinct peak during the dry season and a trough in the early wet season. Temporal segregation in the fruiting seasons of different species tends to occur. The reliance by most of the species studied on a relatively narrow suite of frugivores involves potential interspecific competition for dispersal agents, which temporal segregation of fruiting seasons would minimise (Snow, 1966).

Variations in fruit quality may also reflect the consequences of interspecific competition, resulting in the exploitation of a suite of more dependent, specialized frugivores (McKey, 1975). The lack of clear differentiation in the sets of frugivores exploiting different quality fruit crops, and the dependence of the majority of plants on a few common frugivores suggest that coevolution between fruits and frugivores in this community is in an intermediate stage.

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Are Seed Caching Systems Co-Evolved?

Russell P. Balda

Since the 1960s numerous authors have called attention to the patterns of coevolution that exist between plants and animals. Seeds, however, have been viewed mainly as a source of energy and nutrition for birds and in most graminivorous systems birds are primarily seed predators.

In some instances, however, seed predators are also the chief dispersal agents of the plants upon which they feed. Some birds cache seeds when crops are large. Animals that perform this type of food-hiding have been called "scatter-hoarders" (Janzen, 1971). Here I deal with a small group of temperate-zone corvids (Turcek & Kelso, 1968), species that hoard seeds but certainly do not scatter them. Just the opposite occurs, as the seeds are concentrated in specific sites where they are (a) accessible to the cacher at a later time, (b) defended from other competitors, or (c) not accessible to other competitors because they are well hidden.

Caching species of corvids are in all cases seed predators and potentially dispersal agents. If the bird has the ability to recover and eat all caches, it is a seed predator. If some of the seeds are not recovered and germinate, the system may be a mutualistic one.

In order for a mutualistic relationship to exist both bird and plant must receive greater benefits in reproductive output because of the relationship than could occur without it. The benefits to the plants should include better germination and survival from cached seeds than from ones dispersed by other means. The benefits to the bird must be a reasonably predictable energetic return on its investment of time and energy in caching.

Table 1: Features of pines with different dispersal strategies

Characteristic	*P. ponderosa* (w)	*P. edulis* (a)
Seed size	small	large
Seed conspicuous	no	yes
Seed quickly released	yes	no
Seed coat labelled	no	yes
Synchronous cone opening	yes	no
Position of cone	down, out	up, out
Cone scales	present	absent

The tree

The efficiency of seed dispersal is directly correlated with the bird's ability to harvest and cache seeds. Thus, trees should possess specific adaptations to attract birds to them and make the harvest of seeds as easy as possible. Vander Wall & Balda (1977) compared several characteristics of a wind-dispersed pine (*Pinus ponderosa*) to one (*Pinus edulis*) dispersed chiefly by jays, nutcrackers and mammals (Table 1). The wind-dispersed pine has

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many characteristics to ensure a quick release of small, cryptic, winged seeds from downward facing cones with spines, whereas the animal-dispersed pine has wingless seeds that are "labelled" edible and inedible, and that are held in conspicuous cones that contain no spines. Seeds of bird-dispersed pines are relatively large but have relatively thin seed coats compared to wind-dispersed seeds (Figure 1). Recent studies by TOMBACK (in press) on the relationship of *Nucifraga columbiana* to *Pinus albicaulis* and by MATTES (1978) on *Nucifraga caryocatactes* and *Pinus cembra* reveal many of the same traits. The above characteristics provide no evolutionary guarantee, however, that all the seeds harvested will not be consumed. LIGON (in press) and I believe this happens in the following manner.

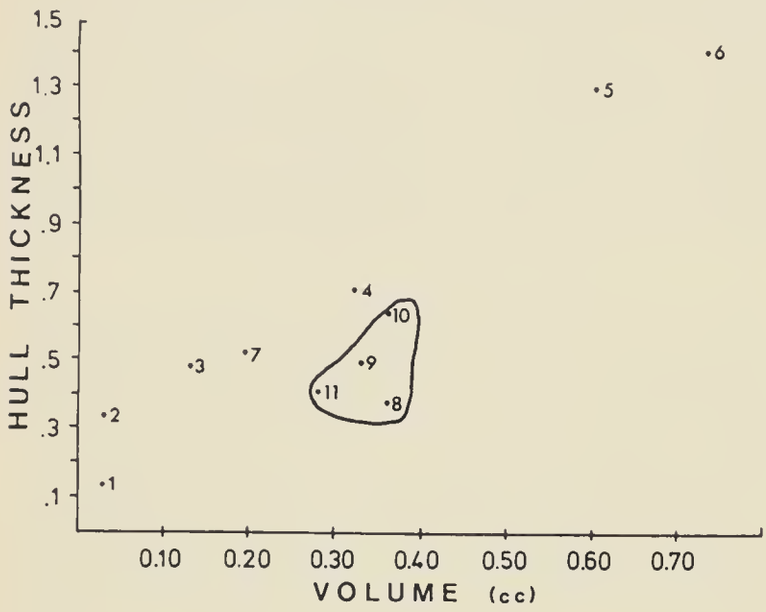

FIGURE 1. Comparison of seed hull thickness and seed volume for 11 species of *Pinus*. Numbers represent the following: 1. *P. aristata*, 2. *P. ponderosa*, 3. *P. flexilis*, 4. *P. coulteri*, 5. *P. pinea*, 6. *P. sabiniana*, 7. *P. jeffreyi*, 8. *P. edulis*, 9. *P. siberica*, 10. *P. cembra*, 11. *P. albicaulis*.

The trees must be synchronized to produce vast crops of seeds in some years which "swamp" the birds and change them from predators to dispersal agents. Those trees out of synchrony will have their seeds eaten rather than cached. The bird pines (and some oaks) all seem to be erratic in their production of seeds, having huge crops in some years and no crops other years, whereas wind-dispersed pines produce a more even supply of seeds (LARSON & SCHUBERT, 1970).

How are the trees cued to produce seeds in synchrony? Botanists have long held that physical factors determine seed set, but microhabitat differences will cause asynchrony if the physical environment is the principal component determining seed set. The needed materials and energy for seed formation are stored in the roots and if the roots are grafted together, as has now been shown for some members of the genus *Pinus* (BORMANN, 1966), then inter-tree communication can occur and seeds may be formed when there is ample energy for all trees to produce a bumper crop. Another unanswered question is: Over how broad an area must the cone crop be large enough to entice storage rather than immediate consumption by the birds?

The interval between cone crops is also critical. Too short an interval may mean that the trees produce a crop of low amplitude and the seeds are all destroyed. Too long an interval may mean the birds are not available as they may have died, left the area, or switched to a different food source. The mean life span of a Piñon Jay is 6.5 years, with most of the mortality falling in the first year of life (BALDA, unpubl. data). The long-term mean for the production of bumper crops of Pinyon Pine seeds is about once every 6 years, with

intermediate crops every 3 to 4 years. Older birds, then, will experience more than one cone crop in their life time (Figure 2).

Pine seeds cached by nutcrackers are usually planted in clumps varying from 2 to 48 (BIBIKOV, 1948; EGOROV, 1961), but the average number is about 12. Only one plant will grow to maturity from those caches not harvested. It is well known that harvesting birds concentrate their efforts on single trees sequentially. If seeds from the same tree are always cached together then intra-cache competition would be most severe between siblings. It has been proposed (MATTES, pers. comm.) that the young seedlings form root grafts among themselves shortly after germination. Because of similar genetic make-up seedlings from the same parent tree may form grafts more easily than seedlings from different trees. This might result in early differential mortality between individuals of the same cache. Three to four years later (BALDA, pers. obs.) all but one shoot may simply be pruned.

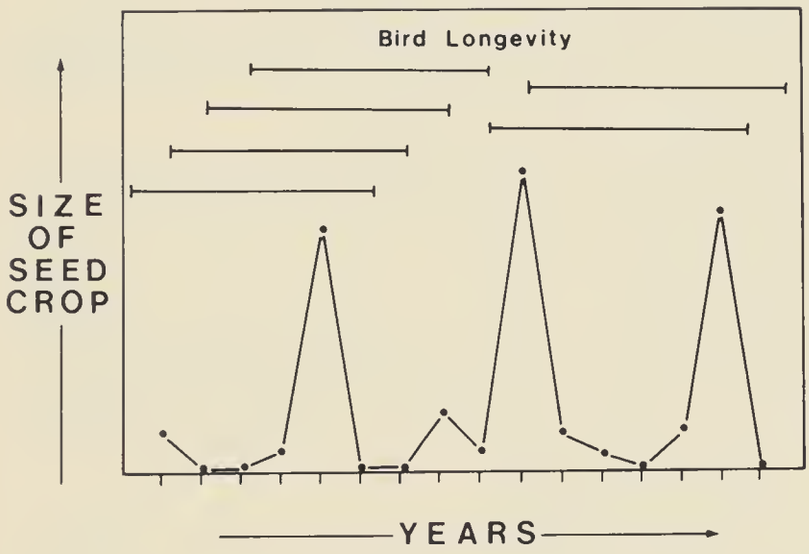

FIGURE 2. Generalised model showing the overlap of huge seed crops of Pinus edulis and longevity of the Piñon lay.

The birds

Seed-caching corvids vary immensely in their behavioral, morphological and physiological adaptations to the seed-caching way of life. Possibly those species with the fewest adaptations (i.e. numerous jays in north and central America) are seed predators under most conditions and only rarely if ever act as dispersal agents.

Morphological adaptations for the caching mode of life are not widespread in the family Corvidae and are best developed in the nutcrackers (BOCK et al., 1973; LÖHRL, 1970).

Physiological adaptations to seeds have been little studied except in the Piñon Jay where LIGON (in press) has shown experimentally and in field studies that in the presence of abundant pinyon pine seeds extensive testicular development sometimes occurs before the winter solstice. This may explain why courtship is initiated during short photoperiods (BALDA & BATEMAN, 1972). Although similar experimental studies have not been done on nutcrackers it is probable that similar results would be obtained. In years of bumper pinyon pine seed crops Piñon Jays in central New Mexico (not known elsewhere) initiate breeding in autumn (LIGON, 1971). Green cones provide the proximal cue for such breedings (LIGON, 1974). The timing of spring breeding in the Piñon Jay is determined by the abundance of pinyon pine seeds the previous fall but it is yet unclear with 7 years of

data if the quantity of seeds is directly correlated with clutch-size. (LACK, 1954, presents limited data from SWANBERG on *N. caryocatactes* showing higher clutches with larger cone crops.) Slightly larger clutches (+ 1 egg) may occur in years of good seed crops but the major trade-off appears to be early nesting and its resultant benefits to reproductive output.

Whole pinyon pine seeds make up about 9% of the food items fed nestling Piñon Jays. The seeds are fed at a rate independent of age and contribute 22% of the protein, 63% of the fat, and 13% of the total carbohydrate intake of the nestling. Nestlings may not survive during the harsh early nesting period without pine seeds in their diet (CLARK, 1978). Digestion of seeds at a very early age is relatively rare in birds.

Behavioral characteristics of seed-caching birds

Birds must be able to recognize the seeds as immediate food and also that this energy source can be stored for later use. Do recognition and storing behavior occur without prior experience? Three pieces of information provide some clues.

(1) Isolated young Piñon Jays hand-reared from 20 days of age began caching seeds and other objects when about 90 days old. Shortly after this, these birds also started filling their expandable oesophagi with seeds (BALDA, unpubl. data).

(2) Cage-raised *Garrulus glandarius* young were isolated from acorns until 150–185 days of age and then given a choice of perching in front of acorns or other similar shaped objects in a balanced design selection experiment. In spite of strong preferences in control runs 5 of 7 birds selected to perch in front of the acorns even though they were not allowed to handle or eat them (BALDA & SJOLANDER, unpubl. data).

(3) In the winter of 1977–78 *N. caryocatactes* invaded Central Europe in modest numbers. Based on plumage, most of these birds were yearlings. Invasions normally occur in years of widespread seed crop failures (FORMOSOF, 1933). There is a good possibility that these birds never saw whole seeds or observed other birds interacting with them. Yet, these young birds appeared to recognize the seeds of *Pinus cembra* instantaneously and began eating, filling their sublingual pouches, and caching seeds immediately (BALDA & CONRADS, unpubl. data).

I conclude that seed recognition and caching behavior occurs in the absence of prior experience and learning in these 3 corvids.

The quality of pine seeds produced on trees varies greatly. Some seeds are partly or wholly destroyed by insects and fungi and some are aborted or never form. Over 3,000 pine seeds have been collected by researchers from nutcrackers and Piñon Jays, and only REIMERS (1959) reports 3 aborted or diseased seeds out of his sample of 500 *P. siberica* seeds. Thus, these birds discriminate edible from inedible seeds.

Piñon Jays (LIGON & MARTIN, 1974) and both species of nutcrackers (VANDER WALL & BALDA, 1977; BALDA, unpubl. data) test each seed with "bill clicking" before depositing some in the throat or pouch and discarding others. A free-flying adult *N. caryocatactes* was provided with unlimited *P. cembra* seeds. The dark-colored rejected seeds were recovered by us after the bird finished all eating and caching activities, and the weight, volume and quality of each of them were compared to a sample of edible seeds. 92% of the

rejected seeds were inedible. Whereas edible and inedible seeds differed only slightly in volume, inedible seeds weighed an average of 0.11 g less than the edible ones ($P < 0.005$). Thus, nutcrackers can discriminate extremely small differences in weight or some characteristics of the seed associated with weight.

Field observations show that vast numbers of seeds are stored in years when seed crops are heavy (Table 2). All conservative calculations (VANDER WALL & BALDA, 1977; TOMBACK, in press; MATTES, MS) indicate that far more seeds are stored than the bird will need to survive the harsh winter.

Observers are always impressed with the industriousness of the birds (SWANBERG, 1950) and the great effort birds will make to obtain the prized seeds. The fixation on pine seeds seems unparalleled in the bird world. I can find no other stimulus object that occurs so irregularly in the life of a bird and yet causes such an overwhelming behavioral response. The mutualistic relationship between the bird and the tree is based, in my view, on this fixation. Given the time, energy and morphological structure for caching seeds it is the motivation or drive that results in the caching of many more seeds than the bird can possibly use.

TABLE 2: Approximate number of pine seeds cached by a single bird when cone crop is high

Bird	tree	number	reference
Gymnorhinus cyanocephalus	*Pinus edulis*	21,500	this report
Gymnorhinus cyanocephalus	*Pinus edulis*	18,000	LIGON (in press)
Nucifraga columbiana	*Pinus edulis*	22–33,000	VANDER WALL & BALDA
Nucifraga columbiana	*Pinus albicaulis*	32,300	TOMBACK (in press)
Nucifraga caryocatactes	*Pinus cembra*	100,000	MATTES (MS)
Nucifraga caryocatactes	*Pinus siberica*	86,000	MEZHENNYZ

The ultimate benefits to the bird occur when the cached seeds are recovered. In order to survive, a Clark's Nutcracker must recover about 1,200 caches of *P. albicaulis* seeds each winter (TOMBACK, MS), or about 850 caches of *P. edulis* seeds (VANDER WALL & BALDA, 1977). This seems an incredibly large number of locations for a bird to remember over a period of months; yet field observations reveal that nutcrackers do so.

TURCEK (1966) concluded that birds cache seeds on familiar terrain, use micro-habitat clues within this terrain and then employ both trial and error and memory when locating caches. TOMBACK (MS) also has compelling field evidence for a memory system but cannot rule out trial and error foraging. Experimental work by BOSSEMA & POT (1974) provides conclusive evidence that the Jay recovers acorns by memory.

Using a semi-tame Eurasian Nutcracker I attempted to determine how caches are recovered. After providing the bird with unlimited access to *P. cembra* seeds for 5 days in a 1.7 x 6.8 m outdoor flight cage the bird was removed for 18 days. In the first 40 min after the bird was returned to the cage it recovered 37 seeds from 12 caches using only 15 different probes (80% success). Later I dug up all remaining caches ($N = 31$ total caches) and measured the area they encompassed (8.7 m^2). A bird can search a maximum of

24 cm^2 with each probe. Thus, the probability of finding a cache by random trial and error foraging is extremely small. Two of the 3 incorrect probes were at locations where the bird had earlier removed the seeds.

In another test I removed the bird after it had made 11 caches. I then dug the seeds up and carefully mapped their locations. The fine sandy floor was then raked and the surface smoothly packed. After 7 days of isolation the bird pecked at 9 of these locations in a 40 min period. Because there was no positive reinforcement the bird now interspersed correct and incorrect probes in an interesting fashion. Even using trial and error search patterns the bird had a foraging efficiency of 51%. Recovery of 81% of the caches by use of trial and error would have required thousands of probes.

In some cases probes were made where a bird had made a cache and then later moved it, and in other cases probes were made more than once at a correct location. This suggests that the bird did not store information about which caches it had harvested or moved. In natural conditions this is not usually necessary as the disturbed soil or snow or the presence of seed hulls next to the cache site indicate that the seeds have been removed. Thus, the memory system is not loaded twice (the location of each cache, and of those caches already consumed).

TABLE 3: Relative characteristics that can lead to a co-evolved system between pine seeds and birds

	eat seed for immediate energy	cache seed for later use
Bird		
1. Size	small	large
2. Energy state	negative to neutral	positive
3. Relative longevity	short	long
4. Residence status	migratory-transient	permanent
5. Ability to find hidden food	poor	good
Environment		
1. Predictability	high	low
2. Harshness	mild	severe
Seed		
1. Amount	rare	abundant
2. Ease of obtaining	difficult	easy
3. Ease of concealing	difficult	easy
4. Size	small	large
5. Permanence of uncached food	high	low
6. Permanence of cached food	perishable	stable

A model for bird-seed co-evolved systems

Table 3 presents a simple model outlining the properties of the bird, tree and environment that probably interact in the establishment and maintenance of bird-seed co-evolved systems.

All species of caching corvids should fall somewhere on a spectrum from complete seed predator to both seed predator and mutualistic species. Ecological conditions will cause a species to shift on this scale from year to year and from locale to locale. One year a species may be a seed predator, the next an efficient dispersal agent.

Small, relatively short-lived species are not candidates for a mutualistic system, for a number of reasons. Small birds must process energy at a relatively constant rate compared to larger species, thus they simply may not have the time to devote to caching seeds. Small birds have shorter life spans and may not live long enough to span the years when seeds are absent. The Piñon Jay, perhaps the smallest mutualistic species, weighs an average of 112 gm.

Seeds should be abundant, relatively large, easy to obtain and conceal, and should remain edible beyond the storage period. The seed hull is important here as thick-hulled are probably more permanent than thin-hulled seeds. Yet if the hull is too thick then the bird may not be able to open it.

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Regional Differences Between Tropical Floras and the Evolution of Frugivory

D. W. Snow

Coevolution between frugivorous birds and their food plants seems to have proceeded more or less independently on the world's main land masses. Starting with different stocks of birds and plants and subject to different climatic and geographical vicissitudes, the outcome as we see it today is quite different in each of the main faunal regions. My aim is to summarise the present situation in the main tropical forest areas, and to see whether the different assemblages of frugivorous birds can be related to regional differences in the tropical floras. The discussion will inevitably be tentative, mainly because the kind of information needed for a thorough investigation does not yet exist.

"Fruit" is often used ambiguously by authors writing uncritically about the food of birds. A distinction must be made between "legitimate" fruit-eaters, which digest the outer part of a fruit and regurgitate or pass the seed intact (in some cases with its ability to germinate improved), and seed predators, which take the fruit in order to digest the seed, often discarding the fleshy parts. Seeds are dispersed primarily by the legitimate frugivores, and it is with them that plants have entered into coevolutionary relationships. I am concerned here only with legitimate frugivores.

A further distinction needs to be made between specialised and unspecialised frugivores. A specialised frugivore may be most simply defined as a bird which feeds only on fruit or is capable of doing so even if occasionally other foods are taken, and also feeds its young mainly on fruit. Coevolution between specialised frugivores and their food plants tends to lead to mutual dependence; the bird depends on the plant for its nourishment, and the plant on the bird for the dispersal of its seeds. The plants involved in such systems are mainly primary forest trees, and their fruits tend to be large, with large seeds and nutritious pericarps. Unspecialised frugivores, on the other hand, eat other things besides fruits, especially insects. They are less dependent than the specialised frugivores on obtaining proteins and fats from the fruit part of their diet. Coevolution between unspecialised frugivores and their food plants has led to less nutritious, smaller, more succulent fruits that are dispersed by a wide variety of frugivores, none of which is dependent on any particular fruit. Among the plants involved in this coevolutionary system are many of the small trees and shrubs of forest edge and second growth. These generalisations have been discussed by several authors (Snow, 1971; Morton, 1973; McKey, 1975). It seems to be a general rule that a comparatively small number of plant taxa have been involved in coevolutionary relationships with specialised frugivorous birds, while many families and genera have coevolved with unspecialised frugivores.

For reasons of space, I omit consideration of the specialised mutual adaptations that have arisen between a few bird groups and the mistletoes (Loranthaceae).

Neotropical Region

In floristic diversity the neotropical forests are rivalled only by those of southeast Asia. In spite of this richness, the number of tree families whose fruits are regularly eaten by

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specialised frugivores is small. The Palmae (palms, at least 9 genera), Lauraceae (laurels, at least 7 genera, many species) and Burseraceae (incense family, at least 3 genera) are of outstanding importance, providing a large proportion of the diet of some of the most specialised frugivores that have been studied. For example, fruits of these three families accounted for over 99% of the food of the Oilbird *(Steatornis caripensis)* in Trinidad over a 4-year period (Snow, 1962), and fruits of the Lauraceae and Burseraceae made up 89% of the diet of the Bearded Bellbird *(Procnias averano)* (B. K. Snow, 1970).

The palms recorded in the diet of specialised frugivores all belong to the cocoid and arecoid sections of the family, which produce fruits with more or less fleshy pericarps, suitable for consumption by birds (Corner, 1966). Except for the atypical genus *Cocos* (coconut palm), cocoid palms are almost confined to the neotropical region (26 genera in the neotropics, 2 in Africa, none elsewhere). The arecoid section of the family is richly represented in both the neotropical and Australasian regions, less richly in the oriental region, and very poorly in Africa.

Other important families for specialised frugivores are the Myristicaceae, Araliaceae, Moraceae and Urticaceae. The last three of these, represented respectively by *Didymopanax, Ficus* and *Cecropia,* are exploited by large numbers of unspecialised frugivores as well as by the specialists; in this they differ from the other families listed above, which mostly produce fruits suitable only for specialised frugivores. Fourteen other families have been recorded in the diet of specialised frugivores, but none of them appears to be generally important.

Many plant families (at least 49) and genera (at least 102), and many fruit types, are represented among the fruits that are eaten by unspecialised frugivores. The Melastomataceae and Rubiaceae are the most generally important families.

The frugivores

Specialised frugivory has evolved in at least 5 neotropical bird families (Table 1). Many other families and genera include species that feed very largely on fruit, and further study may well show that some of these (e.g. some *Turdus* species) should be classified as specialised frugivores.

Among the specialised frugivores, up to 8 cotingas may coexist in the same area (all in different genera), up to 7 toucans (in 3 genera) and up to 6 trogons (in 2 genera). Large numbers of unspecialised frugivores may coexist in the same area, including three or more congeners in such genera as *Turdus, Tangara* and *Thraupis.*

Africa

The African forest flora is notably poor compared with the neotropical and southeast Asian. There are comparatively few tree species, but since many of them are widespread, in contrast to the neotropics and southeast Asia where many species have very restricted ranges, the number of species occurring in any given area may be high (Richards, 1973). The many tree families that are poorly represented in Africa include the two that are most important for frugivorous birds in the neotropics, the Palmae and Lauraceae.

The whole of Africa has only 15 genera and 50 species of palms, compared with 1140 species in the Americas and 1150 in tropical Asia and Australasia. Furthermore, the African palms mostly belong to the borassoid group, with large fibrous fruits unsuitable for birds,

and the lepidocaryoid group, with scaly fruits, which are also mostly unsuitable for birds. The Lauraceae are represented by a small number of tree species, mainly in South Africa and the mountains of East Africa, and a few small shrubs and climbers. The family is poorly represented or locally absent in the Congo forests. I have found no definite record of any lauraceous fruit being eaten by a legitimate frugivore in Africa.

The Burseraceae appear to be of relatively greater importance than the two preceding families. The fruits of at least four genera *(Canarium, Dacryodes, Pachylobus, Santiria)* are eaten by birds in the Guinea forests. In South African forests, on the other hand, the family is absent or represented only by a species of *Commiphora*. *Commiphora*, a genus primarily adapted to arid habitats, has numerous species in Africa and is of great importance to non-forest frugivorous birds.

In marked contrast to these families, the family Moraceae is of outstanding importance in the diet of forest frugivores all over Africa. Indeed one gets the general impression from the ornithological literature that the many species of figs *(Ficus)* are far the most important fruits for almost all frugivorous birds in Africa, with *Musanga* (Urticaceae) possibly in second place in humid areas. Not only do the smaller frugivores, especially barbets, feed very largely on figs, but the much larger turacos do also. This is in striking contrast to the neotropics, where *Ficus* fruits are taken mainly by unspecialised frugivores. *Musanga* is closely related to the neotropical genus *Cecropia* (Janzen & McKey, 1977), and like *Cecropia* its fruits are eaten by both specialised and unspecialised frugivores.

In addition to the families mentioned above, 23 other families are recorded in the diets of specialised frugivores, of which the Annonaceae, Ebenaceae and Euphorbiaceae are among the most important.

As in the neotropics, fruits of many plant families and genera are recorded as eaten by unspecialised frugivorous birds. The Rubiaceae is one of the most important families; the other that is of outstanding importance in the neotropics, the Melastomataceae, is very poorly represented.

The frugivores

Seven African bird families contain specialised frugivores (Table 1), but they are numerically of very unequal importance, and not all are equally specialised. It is noteworthy that the African trogons *(Apaloderma* spp., probably not closely related to the mainly frugivorous neotropical trogons) are entirely insectivorous.

Among the specialised frugivores, up to 10 species of barbets may coexist in the same area, up to 4 species of turacos, and 3 of hornbills. Larger numbers of unspecialised frugivores may coexist in one area, but their numbers are far below the numbers commonly occurring together in the neotropics. African unspecialised frugivores belong to a few other families besides those listed in Table 1 – Pycnonotidae, Turdidae, Timaliidae, Zosteropidae and Ploceidae, of which only the first two contain more than one or two sympatric fruit-eating species.

Southeast Asia

A most important feature of the evergreen forests of southeast Asia is the high proportion of large trees of the family Dipterocarpaceae, whose winged, wind-dispersed

Table 1: Specialised frugivorous birds of the four main tropical forest regions (excluding mistletoe specialists)

Family	Specialised frugivorous genera	Remarks
Neotropical Region		
Cracidae	*Aburria*	Mainly seed predators, but at least one sp. (*A. jacutinga*) regurgitates palm seeds intact
Steatornithidae	*Steatornis*	
Trogonidae	*Trogon, Pharomachrus*	Diets supplemented with insects
Capitonidae	*Capito, Eubucco, Semnornis*	
Ramphastidae	All five genera	Some, perhaps all, supplement diets with animal matter
Cotingidae	*Tijuca, Cotinga, Xipholena, Lipaugus, Cephalopterus, Perissocephalus, Gymnoderus, Procnias, Rupicola*	List probably incomplete. *Procnias* and perhaps a few others exclusively frugivorous; others supplement diets with insects
Pipridae	*Pipra, Manacus, Chiroxiphia*	Less specialised than the cotingas (some insects)
Africa		
Accipitridae	*Gypohierax*	Specialist on palm fruits (*Elaeis* and *Raphia*), but feeding method not typical of frugivores
Musophagidae	*Musophaga, Tauraco, Corythaeola*	
Coliidae	*Colius*	Diet supplemented with other vegetable matter
Bucerotidae	*Ceratogymna, Bycanistes*	Smaller hornbills (*Tockus*) are mainly insectivorous
Captonidae	*Lybius, Stactolaema, Gymnobucco*	
Sturnidae	*Poeoptera, Onychognathus, Cinnyricinclus, Lamprocolius*	
Estrilididae	*Nigrita*	Apparently *N. canicapilla* only
Southeast Asia		
Columbidae	*Ducula, Ptilinopus*	Other genera are seed predators
Bucerotidae	*Aceros, Anthracoceros* etc. (probably all large hornhills)	Diets supplemented with animal matter
Eurylaemidae	*Calyptomena*	Other genera are insectivorous
Irenidae	*Irena*	Other genera are insectivorous
Sturnidae	*Aplonis*	Other genera are partly insectivorous
Australasia		
Columbidae	*Ducula, Ptilinopus*	Other genera are seed predators
Bucerotidae	*Aceros*	
Sturnidae	*Aplonis, Mino*	
Oriolidae	*Oriolus*	
Corvidae	*Corvus, Gymnocorvus*	*C. fuscicapillus* in New Guinea; not other *Corvus* spp.
Paradisaeidae	*Manucodia, Phonygammus, Macgregoria, Astrapia, Parotia, Pteridophora, Paradisaea*	Other genera are largely or mainly insectivorous
Meliphagidae	*Melipotes*	Other genera are mainly nectarivorous and insectivorous

fruits are unsuitable as food for legitimate frugivores. The forests are, however, floristically extremely rich, so that among the other families there are many genera with fruits suited to frugivores. All the tree families that are important for specialised frugivores in the neotropics are well represented. The Arecoid section of the palm family is represented by 13 genera (compared with 34 in the neotropical and 48 in the Australasian regions), while the smaller Caryotoid section (3 genera only), also with drupaceous fruits, is confined to southeast Asia and Australasia.

Detailed information on the identity of fruits eaten by frugivorous birds in southeast Asia is unfortunately still scanty. Palm fruits of at least 3 genera are, however, reported to be eaten by birds, and lauraceous fruits of 4 genera. The Burseraceae appear to be important *(Canarium* and *Santiria* spp.), and in the Myristicaceae various *Myristica* spp. As in African forests, figs *(Ficus* spp., Moraceae) seem to be generally very important.

The frugivores

Specialised frugivory occurs in five families (Table 1). The fruit-pigeons are represented by the same genera as in Australasia, but with smaller numbers of species. Of the broadbills (Eurylaemidae), the only Oriental family at all closely related to frugivorous neotropical cotingas and manakins, only one genus *(Calyptomena)* is a specialised frugivore, the others being insectivorous. In the leafbirds (Irenidae), the only exclusively Oriental bird family, only the genus *Irena* is a specialised frugivore, the others being insectivorous.

There are a large number of unspecialised frugivores in several families, especially Capitonidae, Turdidae, Oriolidae, Sturnidae, Pycnonotidae and Zosteropidae. It is noteworthy that the barbets, though they take much fruit, seem to be more generalised feeders than in Africa (no genus of barbet is common to the two regions). As in Africa, the trogons (all of the genus *Harpactes)* are mainly insectivorous.

Australasia

The forests of New Guinea and northeastern Australia are comparable with the neotropics in their richness in trees suitable for specialised frugivores. The are very rich in palms, especially of the Arecoid section, and also in Lauraceae. (The family Dipterocarpaceae is relatively unimportant.)

Comprehensive information on the fruits eaten by specialised frugivorous birds is limited to studies of fruit-pigeons in Queensland and New Guinea (Crome, 1975a, 1975b; Frith, Crome & Wolfe, 1976). Unfortunately only fragmentary data are available on the diets of the other very important family of frugivores, the birds of paradise (Paradisaeidae). Fruits of six genera of palms and six genera of Lauraceae are recorded in the fruit-pigeons' diet. Other important families are Burseraceae, Myristicaceae and Araliaceae. *Ficus* spp. (Moraceae) are very important in the diets of both fruit-pigeons and birds of paradise.

The frugivores

Several frugivorous groups are shared with the Oriental region (Table 1). Fruit-pigeons are much more numerous in species. In addition, three species of orioles seem to be specialised frugivores, two of crows, and one honeyeater; which suggests that conditions

are more favourable for specialised frugivory in the Australasian than in the Oriental region. The most striking difference, however, is the presence of the large and mainly frugivorous family Paradisaeidae, centred on New Guinea. Up to 12 species of fruit-pigeons may coexist in one area, and probably up to 7 species of specialised frugivorous birds of paradise.

Discussion

The important plant families

Six plant families are generally important for specialised frugivorous birds in all the main regions, with the partial exception of Africa. Two of these (Lauraceae and Palmae) are of outstanding importance in the neotropical and Australasian regions; they are also especially rich in species in these two regions. These are the only two regions where there have been spectacular evolutionary radiations of specialised frugivorous groups (toucans, cotingas and manakins in the neotropics, fruit-pigeons and birds of paradise in Australasia). It is a matter for further enquiry whether the evolutionary radiation of the plants and birds proceeded hand in hand, or whether the radiation of frugivorous birds was made possible by a pre-existing richness in the variety of their food plants.

The principal kind of fruit that is eaten by specialised frugivorous birds is drupaceous, with a layer of firm and nutritious tissue surrounding a single relatively large seed. Botanically such fruits may be berries (Lauraceae, Araliaceae) or drupes (Palmae, Burseraceae), A second type, predominant among the fruits that are less generally important for specialised frugivores, is arillate (e.g. Meliaceae, Myristicaceae). The arils of such fruits are probably rich in fats and proteins (McDiarmid et al., 1977). Fruits of the families Moraceae (mainly *Ficus*) and Urticaceae *(Cecropia, Musanga)* are of very different type, being rather soft with numerous small seeds. The fact that *Ficus* fruits form the staple food of many specialised frugivores in Africa, southeast Asia and Australasia, but not in the neotropics, suggests that neotropical *Ficus* species may have less nutritious fruits than those in the other tropical regions.

The poverty of Africa

The poverty of Africa in the plant families Palmae and Lauraceae seems adequately to account for the fact that there are fewer specialised frugivorous birds in that continent than in the neotropics, southeast Asia or Australasia. Either there has been no striking evolutionary radiation of any group of specialised frugivores in Africa, as there has been in the neotropics and Autralasia; or if there were earlier radiations, they have been followed by extinction. This alternative explanation is mentioned, as it has been suggested that the present African forest flora is an improverished remnant of a much richer flora (Richards, 1973).

Probably as a consequence of the very nutritious fruits that they eat, and of the short time per day that they need spend in foraging, some specialised neotropical frugivores have evolved social systems in which the males are emancipated from the nest and spend most of their time in epigamic display, while the females undertake all nesting duties single-handed. This has culminated in extreme sexual dimorphism, and in the development of leks and other group displays. It is probable that the evolution of the birds of paradise in the

Australasian region was made possible by a similar relationship between the birds and their food supply. Evolution has not, however, proceeded in this way in all specialised frugivorous families; in particular it has not done so in hole-nesting birds such as the toucans, hornbills and barbets, for hole-nesting demands a close pair bond (Snow, 1976). It seems likely that it is the lack, or scarcity, of very nutritious fruits that has prevented any African bird group from evolving along the line taken by the cotingas and birds of paradise. van Someren's account (1956) of the nesting of the turaco *Tauraco hartlaubi* in Kenya is especially interesting in this connection. Both parents fed the young on a variety of fruits belonging to at least eight plant families, of which only one (Moraceae) is among the most important families for specialised frugivores. They brought food about every 15 minutes, regurgitating it in ample quantities to the nestlings. This is in striking contrast to the neotropical cotinga *Procnias averano,* in which a female, feeding its single nestling mainly on lauraceous fruits, brought food at approximately hourly intervals, and was evidently able to collect all that she and the nestling needed in about 10% of the daylight hours (B. K. Snow, 1970).

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Some Evolutionary, Ecological, and Behavioural Correlates of Communal Nesting by Birds with Wasps or Bees

Neal G. Smith

Introduction

Interspecific interactions such as mutualism, commensalism, parasitism, mimicry, and predator-prey relationships reach their highest development in the tropics. Many of these relationships not only cross phyletic lines within the animal kingdom, but also encompass very complex plant-animal associations. Why these interactions should be so relatively dominant in the tropics as compared to the higher latitudes is not immediately evident, nor will I attempt to address that point here. Some have suggested that in areas of high physiological stress, selection is largely governed by physical factors, but in low-stress areas (i.e., the tropics) selection results in biologically accommodated communities produced by past biological interactions and competition (Sanders, 1968). As Dobzhansky (1950) put it, "Where physical conditions are easy, interrelationships between competing and symbiotic species become the paramount adaptive problem."

This paper presents observational and experimental data which affirm that interrelationships between and among species in the tropics may indeed be almost bewilderingly complex. I have studied an association of rather diverse animals for 13 years in Central and South America. It consists of a group of colonial icterids, the oropendolas and caciques; several avian brood parasites, namely two icterids (cowbirds) and three cuckoos, a group of six tyrannid flycatchers which are both parasitic and nonparasitic; an assemblage of vertebrate predators which affect all of the above, almost exclusively during their nesting period; an array of ectoparasitic flies and mites which cause major mortality to all the birds in the association; and a variety of stingless but biting bees, and stinging wasps and ants which exert a major effect on the relationships among and between all of these animals.

Because I started with the oropendolas and caciques, I have tended to treat them as the central species in the association (Smith, 1968; in press). I will continue with this bias because I know more about them than I do, say, about the mites which are both friends and enemies of the oropendolas. I will proceed from the most general to one of the more specific aspects of the association by firstly summarizing the major interactions among all the groups and then dealing more specifically with the case of the colonial icterids and their stinging or biting associates. Finally I present data from experiments which provide some insight into the most specific aspects of this bird-hymenoptera association.

The association in general

Why nest togester?

Predation of eggs or chicks is perhaps the single most important source of mortality for birds breeding in the lowland tropics. Compared to birds breeding in the North Temperate Zone, the fledging success of tropical birds is extremely low (e.g. Ricklefs, 1969), but

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adults have long lives (e.g. Snow & Lill, 1974). Tropical birds appear to have responded in several ways to nest predation, but only one will be considered here: the formation of visually conspicuous intra- and interspecific nesting associations at sites which are relatively predator proof.

The most protected sites are tall, umbrella-shaped, trees containing biting ants (*Azteca* spp.), stinging wasps (*Polistes* spp., *Polybia* spp., *Protopolybia pumila, Stelopolybia areata, Synoeca* spp., etc.) and/or stingless but biting bees (*Trigona* ssp.). The *Trigona* ssp. generally nest in huge, fortress-like nests of *Nasutitermes* spp. termites (Michener, 1974). The chief enemy of the wasps are army ants, *Eciton* spp. (Jeanne, 1975), and the *Azteca* ants effectively repel them. The wasps in turn provide the *Azteca* with protection against anteaters *(Tamandua)*. Anteaters are capable of tearing apart even the concrete-like *Nasutitermes* nest, but flee when attacked by the *Trigona* (personal observation). As I have previously indicated (Smith, 1968), *Trigona* bees which nest in arboreal termite nests are perhaps the best protective agents that a bird could seek against vertebrate and invertebrate predators in the Neotropics. They are easily upset, and will attack in huge numbers even in total darkness.

Sites such as I have described are a limited resource for birds, and usually contain nests of at least two species, and often many more. The oropendolas and caciques, while omnivorous, concentrate chiefly on fruit, a resource for which the strategy of intraspecific territoriality is ill suited. This factor, and predation pressure, results in their colonial nesting habit at "safe" sites. As many as three species of oropendolas and caciques may place their long, bag-like nests (up to ca. 150 nests) either directly around a bee or wasp nest, or at the tips of the terminal branches. Vertebrate predators like opossums, snakes, toucans, and even bats apparently find it difficult, but not impossible, to reach nests in such sites. Up to six species of tyrannid flycatchers may join the icterids at such sites, but they are intraspecifically territorial and usually only one pair per species breeds in any one tree.

Yet pressure from animals which kill their prey immediately is not the only reason for nesting with stinging or biting hymenoptera. The chief source of mortality among the colonial icterids, and perhaps the most important for the tyrannids too, results from ectoparasitic flies of the genus *Philornis* (Smith, 1968; in press). The following appears to be the rule for both colonial and noncolonial species associated with hymenoptera (but not termites): the nearer a bird's nest is to the entrance of wasp or bee nest, the less likely are the chicks to suffer parasitism by *Philornis*. This point will be discussed later.

Consequences of nesting together

The colonial icterids present a tempting target for a variety of other species besides the botflies. The brood parasitic Giant Cowbird *Scaphidura oryzivora* appears to be completely dependent on the oropendolas and caciques, and has formed a highly specialized mutualism with them. Table 1 summarizes some of the aspects of this association. Another cowbird, *Tangavius aeneus*, also parasitizes them, particularly the smaller caciques, but this species has not evolved any of the specializations shown by *Scaphidura*.

Five of the six very similar yellow-breasted tyrannids *(Myiozetetes similis, M. cayanensis, M. granadensis, Coryphotriccus parvus, Pitangus sulphuratus)* use the same grass-like material to build their domed nests. When these species breed close to each other, they

actively steal nest material from one another. Under such conditions, *M. cayanensis* apparently never builds a nest but steals a completed or nearly completed one, usually from *M. similis*. Sometimes two of these species share the same nest, using different entrances. The normal clutch size in these flycatchers is two, but three- and four-egg clutches are common in communal trees. This, and that I have seen *P. sulphuratus* feeding fledglings of either *M. similis* or *cayanensis*, suggests that one or two of these species become brood parasites under these conditions.

TABLE 1: A partial summary of the behavioural, ecological, and evolutionary consequences of nesting with or without stinging or biting hymenoptera. The hosts are the Neotropical colonial nesting icterids, the oropendolas and caciques.

	Host colony with wasps or bees	Host colony without wasps or bees
A.	Wasps/bees provide hosts with protection against ectoparasitic flies *(Philornis)* and vertebrate predators	Hosts are open to attack by flies and vertebrate predators
	thus	**thus**
B.	Hosts discriminate against parasitic cowbirds	Hosts accept parasitic cowbirds
	because	**because**
C.	Cowbird chicks outcompete host chicks and lower hosts' fitness	Single cowbird chicks increase host fitness by removing parasitic fly larvae from host chick
	but	**but**
D.	Wasps and bees often desert site and hosts are then open to attack by flies and vertebrate predators.	When food is limited, two or more cowbird chicks decrease host fitness despite eating fly larvae.
E.	Host colony functions only when wasps/bees are active, and thus get but one chance per year to reproduce.	Host colony is independent of wasps/bees, and has two or more chances to reproduce per year.
F.	Too many nests around a wasp or bee colony may cause the branch to break with a total loss to all.	No such danger.

Host chick fledging rate varies in both situations from year to year, but on the average both are equally successful.

These observations suggest one possible pathway whereby brood parasitism might have evolved. Away from such communal nesting areas, these same flycatchers are themselves heavily brood parasitized by the cuckoos *Tapera naevia* and *Dromococcyx phasianellus*. In communal situations they are seldom parasitized by *Tapera* and never by the forest-dwelling *Dromococcyx*.

The sixth flycatcher, the Piratic Flycatcher *Legatus leucophaius*, provides the link to the colonial icterids because it never builds a nest, but forces a female cacique or oropendola to give up hers. *Legatus* also steals nests from other flycatchers. This is a peculiar species, for while it is highly frugivorous, it is also very territorial and I have never seen more than one pair in any oropendola or cacique colony. Nests were not the limiting resource and it was not clear what *Legatus* was defending.

Colonial icterids and the hymenoptera

Oropendolas and caciques normally returned to the same breeding site every year. Those which were traditionally associated with wasps or bees waited until the insects became active. If the wasp or bee nest was destroyed, the birds abandoned the site. But for several reasons not all of the colonial icterids associated with stinging or biting hymenoptera. Firstly, although most sites with the proper physical characteristics and a wasp or bee nest were occupied, merely being present in such a tree did not guarantee freedom from botflies. Chicks in nests more than 3 m from the wasp nest were often parasitized (Smith, 1968). *Trigona* bees provided the best protection because they tended to swarm over the entire crown of the tree, while wasps tended to be at their nest or away from the tree entirely. Secondly, there were several distinct disadvantages to being addicted to wasps or bees (Table 1, D to F). Thirdly, there were distinct advantages to avoiding the hymenoptera, but such a strategy depended heavily on forming a very tenuous mutualism with the brood parasite *Scaphidura* (Table 1, second column). Some cowbirds were "prudent" in that they placed only one egg in a host's nest (the "mimic type" *Scaphidura*), but others ("dumper type" *Scaphidura*) were not so inclined, and laid not only in empty nests but in those with one or two eggs (Smith, 1968). In heavily parasitized colonies this resulted in many nests having more than one cowbird chick. Although the cowbird chicks preened bot larvae from the host (an advantage for the host), and from themselves as well (an advantage for the cowbirds), they usually outcompeted the host chick for food. The advantage for the host to have them was negated.

Clearly, the host females in colonies lacking wasps or bees should have allowed one, and only one, cowbird egg into their nests. They did not display this degree of sophistication. The dichotomy in their behaviour was of a cruder nature. They either accepted or rejected the cowbirds, depending on the situations outlined in Table 1.

In an experiment which took eight years to complete, I cross-fostered host chicks between the two different colony situations and recorded their behaviour towards cowbirds and cowbird eggs when they became adults. The results were surprising: the hosts did not inherit the behavioural disposition of rejecting or accepting cowbirds, they apparently learned it (Smith, in press). But I do not know how the hosts "learn" the reaction towards cowbirds which is "appropriate" to their nesting situation. The presence or absence of wasps or bees seemed to have been the pivotal variable.

I removed wasp and bee nests with two basic results. If the wasps or bees were removed early in the birds' nesting cycle, the birds simply deserted the colony site. If the insects were removed when the birds had eggs, they behaved as if the wasps or bees were still there and continued to discriminate against the cowbirds. Botflies entered these colonies within a day of the removal of the wasps or bees. In a few cases I was able to transfer branches to which were attached wasp nests (but not *Trigona* nests) into colonies lacking wasps or bees. The birds behaved as if the wasps were not there and continued to accept cowbirds. In no case did the wasps, in the next season, return to where I had transplanted their nest.

Five natural changes in a whole colony's behaviour toward cowbirds occurred in nine years. A change in the breeding site was always involved. Those which became rejectors of cowbirds (3) associated with wasps or bees, while those which changed to acceptors, established themselves in sites lacking hymenoptera. The exact details were not known.

Questions

1. What is the nature of the wasp/bee versus ectoparasitic fly interaction? Why did the presence of these hymenoptera in an oropendola or cacique colony give the birds some protection against *Philornis* spp. flies? I have previously suggested (SMITH, 1968) that the wasps, at least, might prey upon botflies but I now conclude that there is no real evidence to support this idea. The following discussion and Table 2 are but brief summaries of a long series of observations and experiments.

TABLE 2: A summary of reactions displayed by colonies of stingless bees *(Trigona* spp.) and stinging wasps *(Protopolybia pumila* and *Stelopolybia areata)* to *Philornis* spp. flies of both sexes which were tethered in cheesecloth bags. Controls were bees or wasps from the same colonies, adult nymphalid butterflies *(Anartia)*, and empty cheesecloth bags.

	Stingless bees	Stinging wasps
Fly dead	No reaction	No reaction
Fly alive but >7 m distant	Mild reaction, some swarming, nest entrance guarding	Mild or no reaction
Fly alive and <3 m distant	Strong reaction, attack nondirectional; often attack hosts	Variable, but nest entrance guarded, sometimes violent swarming and stinging of substrate
Fly alive, no wings, >7 m distant	Sometimes swarmed, but "alarm" short-lived	No reaction
Fly alive, no wings, <3 m distant	Mild reaction, nondirectional swarming, short-lived	Some swarming to no reaction at all
Stingless bee, <3 m distant	Reaction variable from none to heavy swarming on bag	A few individuals sit on bag, but leave shortly
Wasp, <3 m distant	No reaction	No reaction
Butterfly, <3 m distant	No reaction	No reaction
Empty bags, near and far	No reaction	No reaction

The natural history and taxonomy of *Philornis* botflies are poorly known. Swarms of up to ca. 30 botflies were not uncommon near nests containing chicks in colonies lacking bees or wasps, but I rarely saw such swarms at colonies with bees or wasps. These were always all-male swarms, and on a quiet day one could hear their buzzing at distances up to 8 m. Females flew into such swarms and copulation took place both in mid air and on branches. Females deposited up to 4 eggs or living larvae on a chick. Chicks with more than 10 late instar larvae usually die. The bot larvae themselves are parasitized by mites which enter the nest on the legs of the adult fly. The mites also parasitize the chicks and, at high densities, cause mortality in both.

I reared adult flies from pupae which I collected from nests, and placed male and female flies in separate cheesecloth bags which I tethered to branches at night in a colony with either a wasp or bee colony. From dawn (ca. 0615) to 0900 hours I recorded the behaviour of both the hymenoptera and the flies (Table 2). The hymenoptera reacted to the flies and not to the controls. The reactions occurred in erratic bursts throughout the observation

period, and seldom lasted longer than 1–5 minutes. The strongest reactions were to winged flies (noisy) tethered close to the nest entrance. Wingless flies (silent) induced a reaction but of lesser intensity. Surprisingly, even during the most violent reactions, the swarming was at random and not at the flies.

Such a reaction is typical behaviour which wasps or stingless bees display towards the countless parasitoids which attempt to gain entrance into their nest (MICHENER, 1974; WILSON, 1971; WEST-EBERHARD, pers. comm.). I concluded that they used both auditory and olfactory clues. They behaved as if *Philornis* flies were wasp/bee parasitoids, which they were not.

2. Why did the wasps and stingless bees not attack the colonial icterids and other avian associates? The answer was straightforward: they did attack them, especially when the birds were building their nests. The sting of wasps like *Protopolybia pumila* is extremely painful to humans but the oropendolas and caciques seemed scarcely bothered by them. Only under very heavy attack did any of the icterids fly off, and then only for a short distance to preen the wasps from its plumage. When *Trigona* bees attacked, all the birds fled, and returned only when the bees had calmed down. By the time the oropendolas and caciques had chicks in their nests, attacks on them had almost ceased. Yet toucans *(Ramphastos, Pteroglossus)* were attacked whenever they entered a colony and usually flew off quickly.

Naked oropendola or cacique chicks did not possess this apparent immunity to wasp stings displayed by the adult. If the bag-like nests were experimentally opened and the chick exposed during a wasp attack, the chicks were badly stung and often died as a result. Most birds which habitually associate with stinging or biting insects have closed or domed nests, almost certainly to protect their chicks (MYERS, 1929, 1935, 1936; MOREAU, 1950; MACLAREN, 1950). Possession of feathers is the obvious variable here, but is the plumage of oropendolas and caciques more impervious to the stings of wasps than that of, say, toucans? I do not know.

One other tantalizing correlate of nesting with hymenoptera should be briefly mentioned: a strong body odor. Adults of the species of oropendolas and caciques which habitually associate with wasps or bees possess a musty body odour, while their close relatives which do not form such associations lack this odour. The odour is associated with the plumage, for naked chicks lack it. The odour is not that of the wasp or bee colony. Species like *Cacicus cela* occasionally formed colonies at sites lacking wasps or bees, but those individuals possessed this odour. I have not yet surveyed the literature to see how widespread this correlation is, but it seems to hold for at least the Icteridae, Tyrannidae and Trogonidae.

3. Do the wasps and stingless bees gain anything from the avian associates? Before a positive answer can be given to this question, it is necessary to indicate that it was the birds that joined the hymenoptera not vice versa. It was the highly territorial tyrannid flycatchers, particularly *Legatus* and *Myiozetetes*, which were the effective protectors of wasps against avian predators of wasp larvae. Oropendolas and caciques fled at the approach of such wasp-eating species as the *Daptrius* caracaras or the kite *Leptodon cayanensis*. But the tyrannids were very vigorous in their attack on these large birds and drove them from the colony site. WINDSOR (1976) has shown that birds may be important predators of wasp nests, as least at certain times of the year.

I do not believe that the protection that birds offered to wasps was a significant source of selection in the evolution of the bird-hymenoptera association, but it cannot but help to maintain it.

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SYMPOSIUM ON
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Phylogenetic Relationships and Rates of Evolution in Birds

Ellen M. Prager and Allan C. Wilson

Introduction

The last two decades have witnessed the development of indirect methods for comparing the proteins and nucleic acids of birds. Such methods as electrophoresis, micro-complement fixation, and DNA hybridization have now been used to compare a wide variety of bird species.

These methods differ considerably in their utility. Electrophoresis is most useful for comparing species whose proteins differ in amino acid sequence by 2 % or less (Wilson et al., 1977). DNA annealing methods are most useful for comparing nucleic acids differing by up to 20 % in nucleotide sequence (Wilson et al., 1977). Micro-complement fixation can be used over the range from 1 % to 30 % amino acid sequence difference (Fig. 1). Consequently, electrophoresis is useful mainly for interspecific and intergeneric comparisons among birds. DNA annealing methods are likely to be most valuable from the intergeneric to the intersubordinal level. Micro-complement fixation has proved useful for quantitating relationships among bird genera, families, and orders.

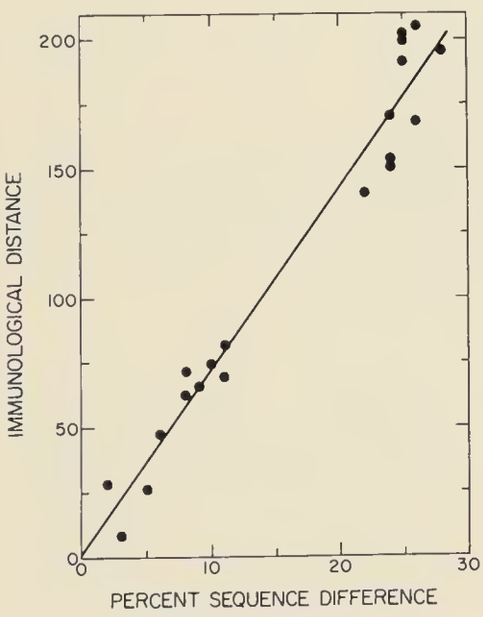

Figure 1. Dependence of immunological distance on degree of sequence difference. Immunological distance was determined by micro-complement fixation. Mammalian pancreatic ribonucleases of known amino acid sequence were compared (Prager et al., 1978). For other proteins the slope of the correlation may differ somewhat, but the linear relationship is maintained (Prager et al., 1978).

All the above-mentioned methods provide quantitative and objective measures of genetic distance among species. These distances may be converted into phylogenetic trees. which depict the probable order of branching and approximate times of divergence of the lineages leading to present-day species.

In the limited space available, we review our own micro-complement fixation work and its bearing on the evolutionary relationships among the higher taxonomic categories of birds. This entails consideration of both branching order and times of divergence among some of the major avian lineages. With the temporal perspective provided

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by the molecular data, we examine rates of evolution at various levels of organization in birds.

Materials and methods

The proteins we have studied most are transferrin, albumin, ovalbumin, penalbumin, and lysozyme. They were compared mainly by quantitative micro-complement fixation, as described previously (Prager et al., 1974 a, b, 1976; Prager & Wilson, 1975, 1976; Ho et al., 1976; Jollès et al., 1976). Fig. 1 gives an example of the empirical finding that this method estimates the approximate degree of sequence difference among related monomeric proteins.

Results and discussion

Phylogenetic relationships

Phylogenetic analysis of the immunological distance data provided by the micro-complement fixation comparisons suggests division of living birds into the following major groups:

1. Paleognathous birds
2. Neognathous birds
    a. Galliformes and Anseriformes
    b. Remaining orders
        i. Miscellaneous land and water birds
        ii. Water birds and owls

Group 1 comprises the 5 orders of paleognathous birds, i. e., the ratites and tinamous. Group 2 includes the remaining 22 orders, which are subdivided into two categories, with subdivision (a) including galliform and anseriform birds and subdivision (b)

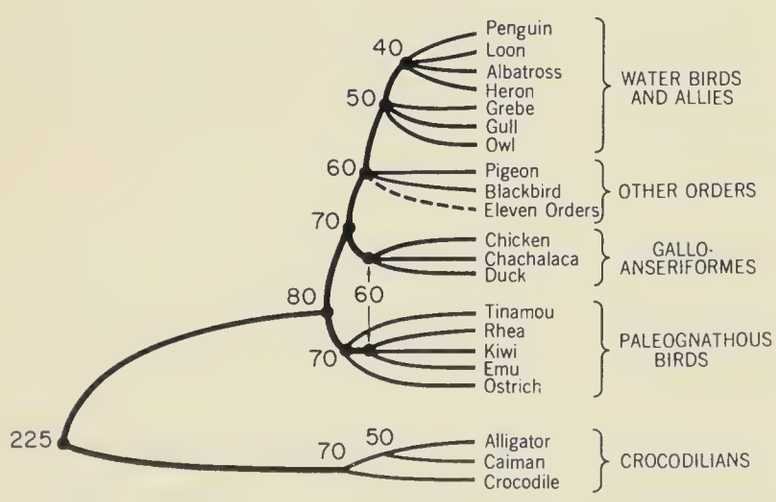

Figure 2. Phylogenetic relationships among bird orders, based primarily on immunological comparisons of transferrin, albumin, penalbumin, and ovalbumin (Prager et al., 1976; Ho et al., 1976; Prager & Wilson, 1976). The results of more limited comparisons of lysozymes c and g, various dehydrogenases, ovomucoid, and cytochrome c were also taken into account. More that 1200 pairwise comparisons were considered, including over 500 transferrin immunological distances. The 11 orders indicated by a dashed line were studied in less detail, antisera to proteins from representative species not having been elicited. Crocodilians (Prager et al., 1974a) are included for comparative purposes. The numbers in the figure indicate approximate minimal estimates of divergence times in millions of years. This tree should be regarded as a suggestion and guide for future research rather than as a definitive statement.

including various orders of land birds as well as a rather tight cluster of water bird orders. Fig. 2 illustrates these proposed phylogenetic relationships.

The water bird cluster became apparent as a result of our collaboration with HO, OSUGA, and FEENEY, who were particularly interested in penguin proteins. By studying several proteins, including the newly discovered penalbumin, we identified loons, albatrosses, and herons as especially close relatives of penguins (HO et la., 1976), with grebe, gull, and owl proteins also quite similar to penguin and loon proteins. It appears likely that a major radiation of aquatic flying birds took place during the Cenozoic era and that penguins and owls are also products of this radiation. These relationships are so close that we expect them to be detected readily by DNA hybridization.

Transferrin evidence indicates that the paleognathous birds constitute a monophyletic group which at the protein level is rather different from all other birds. Evidence for this fundamental cleavage among birds comes also from less complete studies of other proteins (PRAGER et al., 1976). More thorough studies with another protein are needed to test further this hypothesis concerning paleognathous birds. The phylogenetic model in Fig. 2 is consistent with the possibility that there were at least two major phases in the history of birds: the first probably involving an early adaptive radiation of paleognathous birds with limited capacity for sustained flight and the second involving a later adaptive radiation of carinate birds (PRAGER et al., 1976).

Another problem engaging our attention was the relationship of the cracids (e. g., chachalaca) to other gallinaceous birds. Based on lysozyme *c* amino acid sequence work (JOLLÈS et al., 1976) and immunological studies with 3 additional proteins (PRAGER & WILSON, 1976), that relationship, shown in Fig. 2, appears as remote as that between the orders Galliformes and Anseriformes. Sequence data on a fifth protein, ovomucoid, support this conclusion (I. KATO & M. LASKOWSKI JR., pers. commun.). This congruence among the 5 protein phylogenies is impressive and demonstrates the utility of proteins as phylogenetic tools.

Within the phasianoid birds, the turkey *(Meleagris)* is routinely placed in a family or at least a subfamily different from that including the chicken *(Gallus)* and pheasant *(Phasianus)*. Yet, at the protein level, the turkey is at least as close to the chicken as is the pheasant (NOLAN et al., 1975). Additional protein comparisons confirmed this finding (PRAGER & WILSON, 1976). Subsequent morphological comparisons (SCHNELL & WOOD, 1976) also lead one to question the merit of putting the turkey outside the taxonomic group that includes the chicken and pheasant.

Approximate divergence times

Because proteins have evolved at fairly steady rates (WILSON et al., 1977), we have used immunological distance values to estimate approximate divergence times among the major groups of birds referred to in Fig. 2. The fossil record for birds must of course be used to calibrate the time scale. Unfortunately, the avian fossil record is hard to interpret phylogenetically, especially in the Cretaceous era. The fossil evidence that extant orders of birds existed in the Cretaceous period is quite weak (OLSON, 1976). The times given in Fig. 2 are chosen to reflect the fact that hard evidence for existence of present-day orders does not go back far and to reflect estimates that the avian-crocodilian split occurred 225 million years ago (PRAGER et al., 1974 a).

Rates of evolution

Having recognized that proteins behave as approximate evolutionary clocks, we were stimulated to use them as tools for calculating rates of evolution at the supramolecular level. By comparing the proteins of any two species, we obtain an approximate estimate of the time depth separating the two lineages. With this temporal perspective we can estimate the approximate rates at which the two species have diverged at other levels of biological organization.

Hybrid inviability

Our first such effort was estimating the rate at which the potential for interspecific hybridization was lost. We compared the proteins of species known to be capable of producing viable hybrid offspring and converted the protein differences into time. It became clear that many pairs of bird species had retained the ability to produce viable hybrids for more than 30 million years after last sharing a common ancestor. A similar result emerged from comparable studies of frogs. But among mammals, no cases were found in which species separate for more than 10 million years can hybridize. These findings were interpreted to mean that birds and frogs are more conservative than mammals as regards evolutionary change in the systems regulating the expression of genes during embryonic development (Prager & Wilson, 1975).

Chromosomal evolution

We attempted also to estimate rates of evolutionary change in the karyotype of birds. Although it proved difficult to estimate avian karyotypic rates, we have in collaboration with Dr. S. M. Case of Harvard University now devised a satisfactory method, and the results are presented in Table 1. Gross changes in the karyotype appear to have been proceeding more slowly than in an average mammalian lineage but faster than in lower vertebrates, of which frogs are a typical example. It is notable that the mean rate for songbirds is greater than that for other birds. Shields's independent analysis of avian karyotypic evolution (G. F. Shields, this volume) results in a picture consistent with ours.

Table 1: Mean rate of evolutionary change in chromosome number in extant genera

Taxonomic group	karyotypic changes/lineage/million years	
	absolute rate	relative rate
mammals[a]	0.129	100
songbirds[b]	0.037	29
other birds[b]	0.018	14
lower vertebrates[a]	0.009	7

[a] Results taken from Bush et al. (1977).

[b] Results based on analysis by S. M. Case and A. C. Wilson of published information on karyotypic variation within 14 genera of songbirds and 19 genera of other birds representing 10 orders. The average time of first known appearance in the fossil record is calculated from data in Romer (1966) to be 3.75 million years ago for the songbird genera and 9.1 million years ago for the other bird genera.

Karyotypic evolution may be accelerated by the subdivision of populations into demes among which there is little gene flow (LEVIN & WILSON, 1976; BUSH et al., 1977). Within these demes, inbreeding and rapid drift can facilitate the fixation of novel karyotypes. A karyotypic mutation usually has little chance of fixation in a large panmictic population because of heterozygote disadvantage arising from meiotic problems. Thus we infer that bird species may be more highly subdivided than those of most lower vertebrates.

Speciation

Minimal estimates of rates of speciation, in turn, can be made by taking into account the number of species in a taxonomic group and the age of the group. The age can be determined by fossil or biochemical methods. We are currently engaged in such a study. Our calculations to date confirm the widespread feeling among ornithologists that songbirds, especially the nine-primaried oscines, have speciated unusually rapidly. Our biochemical estimate of the age of the group comprising Icteridae + Parulidae + Fringillidae is 10 million years, consistent with the meager fossil evidence (OLSON, 1976). This group contains approximately 850 species. From these two data we calculate by the method of LEVIN & WILSON (1976) that since the common ancestor of this group lived there has been a minimum of 0.9 speciation event per million years in an average lineage. The value of 0.9 is slightly higher than the highest value reported for mammals and exceeds the mean value for lower vertebrates by several-fold (BUSH et al., 1977). Preliminary work with non-passerine groups indicates that here speciation generally proceeds much more slowly, at about the average rate observed in lower vertebrates.

High speciation rates probably reflect a high frequency of founder effects (MAYR, 1970; LEVIN & WILSON, 1976; BUSH et al., 1977). We therefore suggest that the nine-primaried oscines have an exceptional propensity for founder effects by virtue of an unusual combination of two properties: (1) subdivision of the species into demes and (2) capacity of a deme to move as a social unit to a favorable new locality. Subdivision of songbird species into demes is indicated by the phenomenon of local dialects (IMMELMANN, 1975) and by the high incidence of differentiated disjunct populations (ENDLER, 1977).

Morphology

Many vertebrate zoologists have expressed the opinion that anatomical evolution in birds has been slow during the last 30 million years and that in terms of morphology an avian order is equivalent to no more than a mammalian family (PRAGER & WILSON, 1975). By applying numerical methods of morphological comparison such as that introduced by CHERRY et al. (1978) and using proteins as approximate clocks, it should be possible to determine in a quantitative and objective way whether morphological evolution has been slower in birds than in mammals.

If morphological evolution turns out to be slow in birds, it will be consistent with the finding that birds have also been slow with regard to evolutionary change in their developmental systems. In that case we shall be presented with an interesting puzzle because we suspect that some groups of birds, especially songbirds, have speciated rapidly. Perhaps speciation is often a rather superficial phenomenon, involving chiefly

inherited changes in behavior and plumage. The validity of these speculations can be tested by thorough quantitative studies of rates of evolution at various levels.

Concluding remarks

In 1959 Stresemann, a leading student of bird evolution, despaired that ornithologists would ever be able to figure out the phylogenetic relationships among the major groups of birds. Now, we believe, knowledge of these relationships is growing steadily thanks to the advent of new methods. In the last two decades, indirect biochemical methods of estimating genetic distances and phylogenetic relationships among the major avian groups have begun to yield valuable results. With the protein data we have constructed a preliminary phylogeny for the major groups of birds (Fig. 2). This phylogeny deepens our understanding of bird evolution.

Within the next two decades, the indirect methods of macromolecular comparison may be superseded by direct methods. DNA sequencing techniques are improving rapidly (Maxam & Gilbert, 1977; Sanger et al., 1977). They will enable us to make more precise measurements of genetic distance, which will allow significant improvements and refinements in bird evolution.

Acknowledgements

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The Relationships of the "Primitive Insect Eaters" (Aves: Passeriformes) as Indicated by DNA x DNA Hybridization

Charles G. Sibley and Jon E. Ahlquist

Introduction

"In my opinion it is impossible to separate the families Muscicapidae, Sylviidae and Turdidae . . . The so-called muscicapids merge gradually into the so-called turdids . . . What one cannot classify may be considered to be a timaliid . . . So far as we know the separation of the above-named pseudo-families by anatomical characters is as little possible as by external characters." Thus did Hartert (1910, p. 469, translated) express his frustration with the assemblage of passerine birds that have come to be known as the "Old World Insect Eaters" or the "Primitive Insect Eaters".

Hartert (1910) included in his Muscicapidae the muscicapine and monarchine flycatchers, the sylviine warblers, the babblers and the thrushes. As adjacent families he recognized the Accentoridae (=Prunellidae) and the Troglodytidae, in which he included the wrens and the dippers *(Cinclus).*

Hartert's arrangement, which was apparently derived from that of Seebohm & Sharpe (1898—1902), became the foundation for that of Mayr & Amadon (1951) which, in turn, formed the basis for the "Basel sequence" adopted by the editors of the Peters' Check-list (Mayr & Greenway, 1956). The publication of this paper stimulated a series of alternative proposals concerning the classification of the oscines (Delacour & Vaurie, 1957; Amadon, 1957; Wetmore, 1957; Mayr, 1958; Storer, 1959). The debate centered mainly on the sequence of oscine families, especially on the relative positions of the Corvidae and the nine-primaried assemblage.

But there has been more general agreement on the composition of an assemblage of "primitive insect eaters" constructed around the Old World flycatchers, thrushes, sylviine warblers and babblers with included or adjacent groups being the mockingbirds and thrashers, wrens, dippers, accentors, wagtails and pipits. The wagtails and pipits have sometimes been placed near the larks and swallows and sometimes near the nine-primaried oscines. Many recent classifications, including those of Vaurie (1959), Berndt & Meise (1960), Storer (1971), and Voous (1977), have included such a grouping.

Revisions or reviews of some of the constituent groups have been presented by Delacour (1946) for the babblers, Dorst (1950) for the genus *Turdus,* Ripley (1952) for the thrushes, and Vaurie (1952, 1953), Storr (1958), and Traylor (1970) for the Old World flycatchers. Beecher (1953) proposed a radical re-structuring of the oscines based upon his study of the jaw musculature. This revision included splitting the oscines into two superfamilies, Sylvioidea and Timalioidea, which other evidence indicates are members of the same family.

Sibley (1970) reviewed the evidence for an alliance composed of the "primitive insect eaters," added data from the electrophoretic patterns of the egg white proteins, and

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concluded that the muscicapines are closer to the sylviines than to the turdines. This was an error, as will be demonstrated.

The removal of *Zeledonia* from the Turdidae to the nine-primaried assemblage (Sibley, 1968) has been generally accepted as correct, but we will show that *Myadestes* is not closely related to *Phainopepla*, as was suggested by Sibley (1973).

An especially interesting paper by Ames (1975) provides syringeal evidence for a close relationship between thrushes and muscicapine flycatchers and for a low degree of relationship between thrushes and *Prunella*, the babblers, sylviine warblers and monarchine flycatchers. As will become apparent, our DNA data are in good, but not total, agreement with Ames' conclusions.

Materials and methods

The genetic material is deoxyribonucleic acid (DNA) which is a high molecular weight polymer composed of four subunits called nucleotides. The four types of nucleotides differ in the chemical structure of their "bases", namely, Adenine (A), Thymine (T), Guanine (G), and Cytosine (C). The DNA molecule is a double-stranded helix of chains of nucleotides, the two strands being held together by hydrogen bonds between the complementary pairs of bases. In the double-stranded condition A always pairs with T and G pairs with C. Genetic information is encoded in the sequence of the nucleotides.

The two strands of the double-stranded DNA molecule can be separated ("melted") by heating the DNA in solution to a temperature that well dissociate the hydrogen bonds holding the base pairs together. Upon cooling the complementary base pairs reassociate (A-T, G-C) and the double-stranded molecule reforms. This property of "sequence recognition" is the basis of the technique of DNA-DNA hybridization in which experimental conditions are established such that DNA's from two different species are mixed together, "melted" into the single-stranded condition, and allowed to form "hybrid" double-stranded molecules as they cool. The hybrid molecules are then heated and the temperature required to melt them is determined and compared with the melting temperature of reassociated conspecific DNA. The difference is an index to the similarity of the nucleotide sequences of the two species that were hybridized, and therefore to their genetic similarity.

The details of the technique are complex and space limitations preclude an extended description. For further information see Kohne (1970), Kohne & Britten (1971), Britten et al. (1974), and Shields & Straus (1975).

In the present study the DNA of one of the species being compared was "labeled" with radioactive iodine (^{125}I) to permit the amount of hybridization to be measured at a series of 15 temperature steps from 60° C to 95° C as the single-stranded DNA was eluted from a hydroxyapatite column. The frequency distribution of radioactivity is plotted as a curve and the modes of the distributions in ° C are determined. The difference between the modal temperature of the homologous hybrid and that of each of the heterologous hybrids formed with the same labeled species is the delta mode (ΔMd) which is used as a single number comparison. The delta mode is approximately equivalent to the ΔTm (= median temperature difference) of other studies and approximately

equal to the percentage difference of nucleotide pairs between the species being compared (KOHNE, 1970).

The delta mode scale ranges from 0.0 for the score of a homologous hybrid to approximately 20 for the most distant orders of birds. Delta mode values up to approximately 2.5 are usual for congeneric species; from 3.0—9.0 for members of the same family; from 10.0—15.0 for different families in the same order, and above 15 for members of different orders. These values are approximate and, as the present paper will demonstrate, the boundaries of currently accepted "families" and "orders" may be erroneous and cannot be used to calibrate the delta mode scale.

Results

The matrix of delta mode values for 153 pairwise comparisons among 18 taxa is presented in Figure 1. The delta mode values for 11 of these taxa were used to compute the values in the Distance WAGNER Tree (FARRIS, 1970, 1972) of Figure 2. The tree has a total homoplasy value of 86 and the cophenetic correlation coefficient is 0.80 (SNEATH & SOKAL, 1973). The following conclusions are indicated. We have DNA hybridization data for all taxa mentioned. Delta mode values are given in parentheses, e.g. (6.9).

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
Turdinae	* A																		
Erithacus	* B	9.3																	
Myadestes	C	6.9	8.5																
Muscicapa	* D	8.5	6.2	8.3															
Miminae	* E	7.8	8.9	9.2	7.7														
Sturnus	* F	8.3	8.7	9.5	8.2	5.8													
Cinclus	G	9.6	9.8	9.8	9.0	8.9	9.3												
Phainopepla	H	9.4	9.9	11.1	7.8	10.4	8.4	11.3											
Sylvia	* I	10.6	11.1	11.0	9.2	12.5	13.1	12.1	9.8										
Trichastoma	* J	9.6	10.9	10.0	8.8	10.9	11.0	10.4	7.7	7.1									
Chamaea	K	9.6	10.9	10.0	9.2	12.9	13.0	10.4	7.7	8.3	6.4								
Parus	* L	11.5	10.3	11.0	11.4	10.8	10.7	10.8	9.8	8.4	10.2	9.1							
Thryomanes	M	11.2	10.5	11.1	10.7	11.1	10.5	10.7	9.2	12.4	10.4	10.3	10.8						
Prunella	* N	10.7	11.8	11.0	12.2	9.3	10.4	10.8	9.7	12.4	8.5	8.5	12.0	11.6					
Motacilla	* O	10.5	10.3	9.5	9.6	9.7	11.0	11.6	7.6	9.7	9.8	9.0	10.1	10.1	5.6				
Ploceinae	* P	10.5	9.1	10.0	8.6	8.8	9.3	9.7	7.1	8.9	8.4	8.4	10.6	9.0	5.6	5.7			
Monarcha	Q	12.1	11.9	11.4	10.4	10.1	11.2	10.8	9.1	9.3	9.1	9.1	9.5	11.0	9.6	8.3	8.2		
Corvus	R	11.4	10.2	11.5	9.9	11.1	9.9	11.0	12.2	9.0	9.0	9.0	10.3	10.4	13.2	9.8	10.0	5.3	

FIGURE 1. Matrix of delta mode values for 18 taxa of passerine birds. The asterisks(*) indicate the taxa used to calculate the Distance WAGNER Tree in Figure 2.

1. The thrushes, muscicapine flycatchers, mockingbirds, starlings, and dippers are members of a monophyletic assemblage. a) Within this group the muscicapine flycatchers (*Muscicapa, Melaenornis, Niltava, Rhinomyias*) are closely related to the chat-like thrushes (*Erithacus, Erythropygia, Phoenicurus, Luscinia, Cossypha, Pogonocichla, Myrmecocichla, Copsychus*). b) The starlings (*Sturnus, Onychognathus, Spreo, Ampeliceps, Aplonis*) are closest to the mockingbirds and thrashers (*Mimus, Dumetella, Toxostoma, Oreoscoptes*). c) The turdine thrushes include *Turdus, Catharus, Hylocichla, Zoothera* and *Myadestes*. d) *Cinclus* is closer to the thrushes, flycatchers, starlings and mockingbirds than to the wrens.

2. The relationships of the solitaires, *Myadestes*, have been discussed by SIBLEY (1973), who concluded that they were related to the silky flycatchers (*Phainopepla*, etc.). AMES (1975) concluded that the syrinx of *Myadestes* is not typically turdine, but he was unable to suggest an alternative alliance.

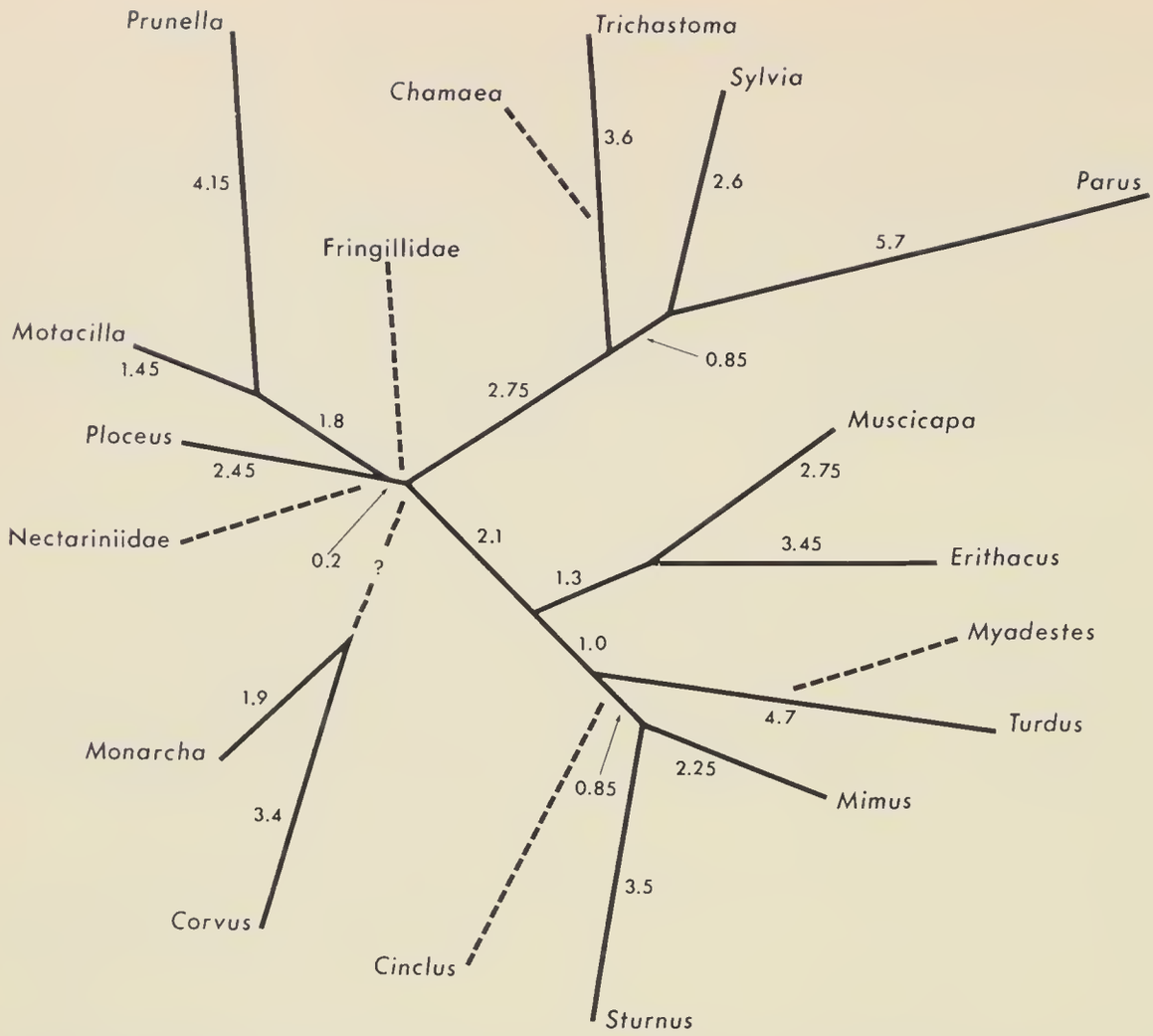

FIGURE 2. Distance WAGNER Tree based upon the delta mode values in Figure 1. The positions of taxa connected by solid lines were determined by a single computer run. Taxa connected by dashed lines were entered separately but their positions are in accordance with delta mode values.

The DNA evidence shows that *Myadestes* is most closely related to the turdine thrushes (6.9) and is quite distant from *Phainopepla* (11.1). In addition to the taxa in Fig. 1 we have examined DNA hybrids between *Myadestes* and representatives of the major groups of passerines. We conclude that *Myadestes* is a turdine thrush, most closely related to such genera as *Turdus, Catharus* and *Zoothera.*

3. *Phainopepla* is closest to *Bombycilla* (4.5) and to *Dulus* (6.7), in agreement with ARVEY (1951) and contra SIBLEY (1973). Additional information on this problem will be published elsewhere.

4. The sylviine warblers, babblers, and titmice are members of a monophyletic cluster but the data are incomplete and other taxa may be involved which have not yet been examined. *Chamaea* is a babbler, close to *Trichastoma.*

5. The weaverbird-fringillid assemblage includes the weaverbirds, estrildines, *Passer,* sunbirds, wagtails and pipits, *Prunella,* and the nine-primaried oscines (=Fringillidae of SIBLEY, 1970).

6. The monarchine flycatchers (*Monarcha, Chasiempis, Trochocercus, Terpsiphone, Philentoma, Hypothymis)* are members of the corvine group and are not closely related to the muscicapine flycatchers. The fantails (*Rhipidura),* whistlers (*Pachycephala),* dron-

gos *(Dicrurus)* and certain other taxa are also members of this group. A more complete presentation of the data will be published elsewhere.

7. The wrens (Troglodytidae) do not show a close relationship to any of these assemblages but a *Thryomanes-Polioptila* DNA hybrid has a delta mode value of 7.1. Additional data are needed to establish the positions of the wrens and gnatcatchers.

8. The Australo-Papuan "scrub-robins" *(Drymodes)* have usually been placed with or near the thrushes (Ripley, 1952, 1964; Mayr, 1963; Schodde, 1975) although Sharpe (1903), Mayr (1941), and Rand & Gilliard (1968) considered them to be babblers.

However, Sibley (1976) suggested that "*Drymodes* is not a thrush but a member of the Australian endemic complex" (p. 569). The DNA data support this suggestion. *Drymodes* is distant from *Turdus* (11.4) and *Erithacus* (11.8) but close to *Eopsaltria* (5.4) and *Poecilodryas* (5.5).

Discussion

The "primitive insect eaters" thus prove to be a polyphyletic assemblage composed of parts of a least four monophyletic groups. We do not yet know the relationships of the Australian "warblers" (*Acanthiza, Malurus,* etc.), the larks, swallows, nuthatches, creepers, bulbuls, kinglets, white-eyes, vireos, and several other groups. But it is already clear that the oscine passerines are far more diverse genetically than they appear to be morphologically and that the present classifications do not reflect their phylogeny.

The pattern of evolution is cladistic, in the sense of Hennig (1966), and adaptive radiation is the usual expression of this process. Thus we should expect to find monophyletic assemblages composed of ecologically and morphologically diverse taxa. The availability of the same or similar ecological niches in different parts of the world produces morphologically convergent taxa from different ancestral stocks. These often deceive the morpho-taxonomist who assembles them into polyphyletic taxa. It is now possible to use DNA hybridization to solve such problems and to provide quantitative answers to phylogenetic questions.

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The Pattern of Uropygial Gland Secretions as a Chemotaxonomic Parameter in Avian Systematics

Jürgen Jacob

Introduction

Based on the first relevant investigation on the chemical composition of the uropygial gland secretion from the common duck by Weitzel & Lennert (1951) a series of papers demonstrated that monoester waxes composed of predominantly unbranched alcohols and fatty acids with a methyl branch at the C-2- (or in some cases at the C-4-)atom and additional branches at other even-numbered C-atoms are characteristic for Anseriformes.

Galliform species show very different preen secretions in that they contain diester waxes composed of alkane-2,3-diols esterified with unbranched fatty acids (Haahti & Fales, 1967; Hansen et al., 1969; Jacob & Grimmer, 1970 a, b). From these preliminary results the hypothesis was born that the uropygial gland wax composition of closely related birds should differ only quantitatively, whereas qualitative differences could be expected in birds belonging to different orders. If the results of this chemical classification would not contradict the natural system, this technique could contribute to avian systematics. In the meantime more than 300 birds belonging to different orders and families have been investigated and the data have confirmed the natural system (Jacob, 1978). Although, as a result of our lack of knowledge of its function, we don't know why the preen wax composition is such a stable species-specific parameter, it seems to be possible to gain insight into relationships among birds by comparing their preen wax compositions. The advantage of the method lies in its relative simplicity and the fact that the structure of the wax pattern can be determined to the molecular level without the complex techniques of sequencing proteins or even nucleic acids.

Material and methods

The procedure of collecting and cleanup of uropygial gland secretions as well as the cleavage of ester waxes, oxidation of alcohols etc. have been published elsewhere (Jacob, 1975, 1976 a). Separation of methyl esters and alcohols, respectively, is performed by gas-liquid chromatography on 10 m glass columns packed with GasChrom Q coated with OV 101, or on 25 m capillary columns using the same impregnation. Identification is performed by comparison of retention times or, better, equivalent chain length and by means of mass spectrometry using the instruments Varian MAT 111 (for packed columns) or Varian MAT 112 S (for capillary columns).

Results and discussion

The following orders have been hitherto investigated (Jacob, 1977 a): Sphenisciformes, Procellariiformes, Podicipediformes, Pelecaniformes, Ciconiiformes, Phoenicopteriformes, Anseriformes, Falconiformes, Galliformes, Gruiformes, Charadrii-

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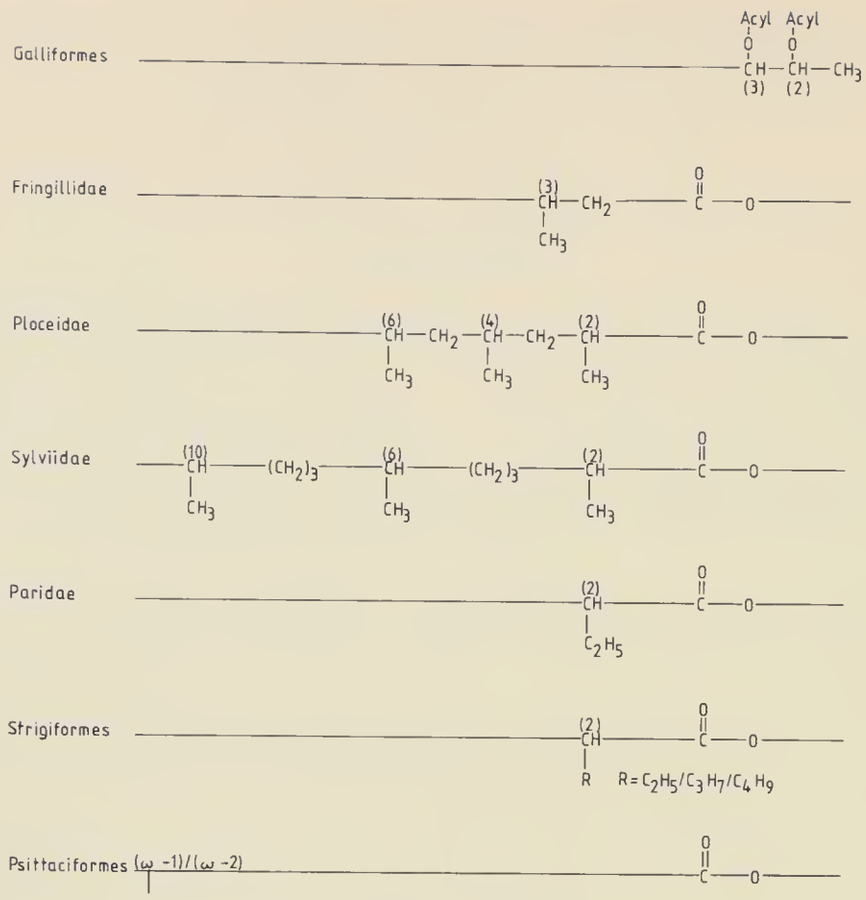

FIGURE 1: Some selected typical structures of uropygial gland waxes.

formes, Lariformes, Columbiformes, Psittaciformes, Cuculiformes, Strigiformes, Coraciiformes, Piciformes and Passeriformes (Corvidae, Sylviidae, Paridae, Fringillidae, Emberizidae, Ploceidae, Estrildidae, Certhiidae, Regulidae, Paradoxornithidae).

Sphenisciformes and Procellariiformes

These two orders show very complex but similar wax patterns. The wax acids belong to a large number of homologous series including 2-, 3- and 4-mono- as well as polymethyl-substituted acids. Two different chemical groups can be distinguished equally in penguins and in tubenoses. The albatross *Diomedea melanophris* seems to be the most atypical procellariiform bird among the species investigated, showing similarities with Lariformes and other orders. Penguins and tubenoses seem to be closely related (JACOB, 1976 b).

Podicipediformes and Pelecaniformes

Grebes show the most complex wax patterns so far investigated. Additionally, non-isoprenoid hydrocarbons have been detected in this order exclusively. The Podicipediformes show close relationship to Phalacrocoracidae (Pelecaniformes) and, moreover, to the penguins and tubenoses.

Ciconiiformes

This order still remains problematic and appears to be heterogeneous in that different families show completely different wax patterns (monoester waxes, diester waxes, triglycerides).

Phoenicopteriformes

The wax from *Phoenicopterus ruber* (Bertelsen, 1970) contains predominantly 2,4,x-trimethyl-substituted acids and thus shows relationship to Anseriformes.

Anseriformes

The large order is characterized by wax acids methyl-substituted at C-2 or C-4 having additional methyl-branches at other even C-atoms. Families can readily be distinguished by the degree of substitution. *Anser, Dendrocygna* and *Cygnus* appear close together if the degree of substitution is compared. *Mergus* is trimethyl-substituted and can be separated from the aforementioned genera but seems to be close to *Melanitta, Cairina* and *Branta* species. *Anas* species are well separated from other anseriform species. *Tachyeres* appears just between *Somateria* and *Anas* (Jacob, 1977 b).

Falconiformes

This homogeneous order is characterized by acids with a first methyl-branch at C-2 and a second at the non-polar end of the molecule. No relationship to other orders hitherto investigated can be suggested.

Galliformes

The diester waxes containing alkane-2,3-diols are characteristic constituents of the uropygial gland secretion from species of this order. They seem to be unique and no relationship to other orders can be detected.

Gruiformes

Preferentially acids with methyl-branches at every fourth C-atom occur in this order. *Rallus, Porzana, Gallinula* and *Fulica* are closely related. The cranes show a lower degree of substitution but are closely related to the aforementioned genera.

Charadriiformes and Lariformes

Although these orders can readily be distinguished, they are obviously closely related. Alcidae are predominantly unbranched but show great similarities with Laridae (gulls). *Chionis* seems to be closer to Lariformes (Jacob, 1977 c), whereas *Thinocorus* is closer to Charadriiformes than to Lariformes.

Columbiformes

Columbiformes can be well separated from all other orders by the occurrence of 3-hydroxy fatty acids as constituents of the preen wax. It should, however, be noted that these acids have been detected in Anseriformes also.

Psittaciformes

Several chemical classes occur in this order. The predominance of acids with methyl-branches at ($\omega - 1$)- and ($\omega - 2$)-carbon atoms characterizes at least some genera.

Cuculiformes and Piciformes

3-Methyl-branched acids predominate in these orders. As this acid type occurs in various passeriform families, Cuculiformes and Piciformes cannot be separated from these families nor from each other.

Strigiformes

Strigiformes are characterized by acids with larger substituents at the C-2 atom (ethyl-, propyl-, or butyl-), a very unusual condition in preen waxes. *Tyto* is different.

Coraciiformes

Only *Alcedo atthis* has been investigated. It shows the most branched wax so far detected.

Passeriformes

Corvidae, Sylviidae, Paridae, Fringillidae, and Ploceidae all show very characteristic wax patterns and thus can readily be distinguished. *Passer* shows a fringillid pattern, not a ploceid one. *Remiz pendulinus, Panurus biarmicus* and *Aegithalos caudatus* are not true tits, but should be placed together with Regulidae, Certhiidae and Paradoxornithidae near to Sylviidae (Poltz & Jacob, 1974, Jacob & Grimmer, 1975).

The general observation was made that phylogenetically old species show very complex wax patterns (Sphenisciformes, Procellariiformes, Pelecaniformes, Podicipediformes)*, whereas the more recent species possess waxes containing acids which belong to only a small number of homologous series (Galliformes, Columbiformes, Piciformes, Cuculiformes, Passeriformes). Charadriiformes, Lariformes, and Gruiformes are located between these extremes. Ploceidae are the most modern family from this viewpoint since they possess a wax consisting of one acid and one alcohol only.

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* However, these orders may be rather young according to Prager & Wilson (1980)

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Avian Cytogenetics: New Methodology and Comparative Results

Gerald F. Shields

Introduction

Most aspects of avian biology are reasonably well known. Studies of bird chromosomes, however, lag far behind those of most vertebrate groups, particularly mammals (Table 1). This lag is based largely on the fact that avian cytogenetic technique has not been well developed. Additionally, the necessary marriages between field oriented ornithologist and laboratory oriented cytogeneticist have not been widespread. Finally, bird chromosomes are inherently difficult to analyze since their number is usually high and most exist as minute microchromosomes barely visible by light microscopy.

The majority of data available suggest that avian chromosome evolution has been conservative in that most birds studied possess similar diploid chromosome numbers (Figure 1) and that little or no karyotypic variation is observed over relatively broad phylogenetic ranges. However, my data of ten years of observation indicate a relatively high degree of chromosome change in some groups, particularly in the passerines. Most groups, however, have not been analyzed with any degree of rigor and far more study is needed before a full assessment of these parameters for all groups can be made.

Table 1: Number of karyotypes described for various vertebrate classes

Class	karyotypes described	percent of total
Mammalia	1 500	37.6
Aves	214	2.5
Reptilia	275	4.6
Amphibia	352	18.0
Osteichthyes	500	3.0

My intent in the present paper is to: emphasize the utility of current avian cytogenetic methodology, relate the results of a number of my studies to our current knowledge of the avian karyotype and finally, comment on preliminary estimates of the extent of chromosome change both within and between species of various avian orders.

Materials and methods

Mitotic analyses

I have routinely obtained excellent karyotypic materials from tissue cultures of avian fibroblasts (Shields, 1973). Sterile tissues are minced in 0.5 % trypsin in saline and dispersed in a stirring flask until homogeneous. Dispersed cells are then collected by centrifugation (800 rpm) and dispersed in 10 ml of 1066 growth medium supplemented with 5 % fetal calf serum and 0.02 % antibiotic-antimycotic. This suspension is then

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innoculated into petri dishes containing sterile glass slides and 30 ml of growth medium. The cultures are then incubated for four days at 38° C with a continuous 5 % CO_2 flush. Colcemid (6 μg/10 ml medium) is added two hours before tissue harvest and the cells are then subjected to hypotonic treatment (3:1, H_2O:medium), fixed in 3:1 methanol-glacial acetic acid, air dried, stained and mounted. This procedure has consistently provided large numbers of chromosome spreads of excellent morphology, an absolute necessity for accurate analysis. In addition, cell lines can be continued in culture for later analysis.

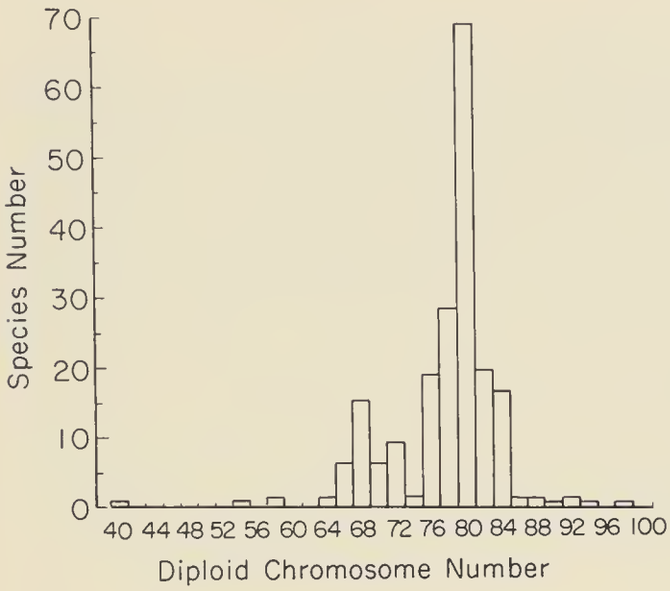

FIGURE 1. Distribution of diploid chromosome numbers reported for birds.

Meiotic analyses

Testes of males actively undergoing spermatogenesis are excised and placed in distilled water at 38° C for 20 minutes. Their tunics are then broken in methanol-glacial acetic acid (3:1) and tissue pieces are then smeared onto albuminized slides and squashed under a coverslip. The coverslips are then floated free in fixative and the slides air dried, stained and mounted. This procedure can be used to great advantage in the field where tissue culture facilities may not be available. Premeiotic mitotic divisions can be obtained from meiotic tissue which has been subjected to colcimide pretreatment (see mitotic analysis). Additionally, rigorous determinations of diploid chromosome numbers can be made since the reduced haploid number of meiotic bivalents can be determined with relative ease. Finally, meiotic chromosome analysis may provide a diagnostic description of chromosome variation which had been previously detected at mitosis.

Differential chromosome banding

Techniques designed to band mammalian chromosomes differentially have been used to great advantage since their introduction nearly ten years ago. These procedures provide intra-chromosomal differentiation which is not detectable by conventional methods. Since avian chromosomes are inherently difficult to pair homologously the advantages of differential banding are obvious. Avian chromosomes have proven difficult to band, but, several techniques (SEABRIGHT, 1972; SHIRAISHI & YOSIDA, 1972; ARNASON, 1974) provide excellent results. I routinely use the trypsin-GKN technique of Arnason which induces giemsa (G) bands.

Fresh (2—4 day old) chromosome preparations are denatured for 10—30 sec. in a solution of trypsin-GKN-versene (6:24:30). GKN is made by dispersing: 10 g. glucose, 4 g. KCL, 80 g. NaCl, and 3.5 g. $NaHCO_3$ in 1 liter of triple distilled water. Slides are then washed in GKN, stained in 2 % giemsa (pH = 6.8), rinsed briefly in tap water and mounted. This procedure provides excellent banded karyotypes but it has been our experience that chromosome preparations older than six months do not band.

Results and discussion

Chromosome variation

The extent of chromosome variability within vertebrate groups has recently been summarized by Bush et al. (1977) and by White (1978). Rapid karyotypic evolution has been associated with organismal diversity in mammals and conversely, slow karyotypic evolution has been associated with organismal similarity in amphibians (Wilson, et al., 1974). No detailed comparative studies of the extent of karyotypic variability in groups of birds are available. The work of Takagi & Sasaki (1974) based partially on comparisons of banded chromosomes suggests that little or no karyotypic variability exists between avian species, indeed even between avian orders. Considerable variability exists between the banded chromosomes of the Ring-necked Dove, *Streptopelia risoria,* and the Domestic Pigeon, *Columba livia,* however (Stock et al., 1974). My published and unpublished data suggest that while the general features of the avian karyotype (diploid numbers and presence of both macro- and microchromosomes) are similar,

Table 2: Intraspecific macrochromosomal variation in birds

Species	order	chromosomal variation	methodology	author
Junco hyemalis *Junco caniceps* *Junco phaeonotus*	Passeriformes Passeriformes Passeriformes	floating pericentric inversions, #2 and #5	Beta** karyology	Shields (1973)
Zonotrichia albicollis	Passeriformes	floating pericentric inversions, #2 and #3	Beta karyology	Thorneycroft (1966, 1975)
Cardinalis cardinalis	Passeriformes	centric dimorphism, #5	Alpha* karyology	Bass (1978)
Chloris chloris	Passeriformes	centric dimorphism	Alpha karyology	Hammar (1975)
Bombycilla cedrorum	Passeriformes	centric dimorphism, #2	Alpha karyology	Thorneycroft (unpublished)
Vanellus vanellus	Charadriiformes	centric dimorphism, #1	Alpha karyology	Hammar (1970)

* Alpha karyology refers to work based on small sample sizes and not accompanied by meiotic studies.

** Beta karyology refers to work based on large sample sizes and meiotic analyses.

chromosomal rearrangement may be extensive in some groups. In light of my earlier work and the associations between chromosome variability and organismal complexity in other vertebrates made by WILSON, it seemed appropriate to assess the degree of chromosomal variability in various bird groups.

My observations of banded chromosomes are restricted to several species and thus comparative data are based on chromosomes stained by conventional methods. Intra- and inter-specific chromosome variability was assessed in 73 species of various avian orders for which appropriate data are available.

Intraspecific chromosome variation

Detailed studies on intraspecific chromosomal variation in birds exist only for the White-throated Sparrow, *Zonotrichia albicollis* (THORNEYCROFT, 1966; 1975) and for species of the genus *Junco* (Shields, 1973; 1976). In the White-throated Sparrow chromosomes 2 and 3 are polymorphic. The ancestral chromosomes 2 and 3 gave rise to the derived chromosomes 2^m (m = metacentric) and 3^a (a = acrocentric) respectively by two separate pericentric inversions. In *Junco* chromosomes 2 and 5 are polymorphic.

TABLE 3: Macrochromosomal variation within 14 genera of non-passerine birds

Genus	age of genus* t	number of species s	chromosome changes Δk	change/ species Δk/s
Aix	1	2	2	1.00
Anser	19	5	1	.20
Aythya	19	2	0	.00
Mergus	1	2	0	.00
Buteo	30	2	0	.00
Falco	19	2	1	.50
Lophortyx	8	2	0	.00
Grus	10	4	0	.00
Anthropoides	1	2	0	.00
Larus	19	4	1	.25
Sterna	19	2	1	.50
Columba	1	2	0	.00
Psittacula	1	3	1	.33
Picoides	1	2	2	1.00
totals	149	36	9	3.78

* According to ROMER (1966).

$$r' = \frac{\Sigma(\Delta k/s)}{\Sigma t} = \frac{3.78}{149} = 0.026$$

r′ is the mean rate of chromosome change, calculated by the method of BUSH et al. (1977).

The ancestral chromosomes 2 and 5 gave rise to the derived chromosomes 2^{sm} (sm = submetacentric) and 5^m (m = metacentric) respectively by two separate pericentric inversions. Intraspecific chromosomal variation has been reported in four other species (Table 2) but the analyses are not rigorous. It is, however, significant that seven of the eight species in which intraspecific variability has been detected are passerines.

Interspecific chromosome variation

In an effort to assess the degree of interspecific chromosomal variation in birds, unpublished data from this laboratory as well as published data from the literature were analyzed. In this analysis only species of the same genus were compared. Comparisons of distantly related species even in the same family were avoided since assessment of interspecific chromosome variability in divergent species may be obscured by multiple overlapping chromosomal rearrangements which can not be detected by these methods. Since detection of homologies among avian microchromosomes even with the use of differential banding techniques is difficult, comparisons were restricted to only the first twelve pairs of macrochromosomes. These methods can detect whole arm fissions or fusions, unequal reciprocal interchanges, centric shifts and pericentric inversions. They do not, however, detect paracentric inversions or equal arm interchanges. The results of these analyses for non-passerine and passerine birds are summarized in Tables 3 and 4 respectively.

Table 4: Macrochromosomal variation within 13 genera of passerine birds

Genus	number of species s	chromosome changes Δk	change/species $\Delta k/s$
Empidonax	4	4	1.00
Parus	2	0	.00
Sitta	2	3	1.50
Turdus	5	2	.40
Oenanthe	2	0	.00
Motacilla	2	3	1.50
Lanius	3	0	.00
Vireo	4	2	.50
Passer	3	2	.66
Carpodacus	2	0	.00
Junco	4	0	.00
Zonotrichia	2	3	1.50
Emberiza	2	0	.00
totals	37	19	7.06

$$r' = \frac{\Sigma(\Delta k/s)}{\Sigma t} = \frac{7.06}{37} = 0.144$$

r′ is the mean rate of chromosomal change, calculated by the method of Bush et al. (1977). The average age of passerine genera was assumed to be 3.75 million years (Romer, 1966).

Chromosomal variability within passerines is clearly higher than that observed in non-passerines. This, coupled with the fact that intraspecific chromosome variability in passerines appears high, argues strongly for differential rates of chromosome change among avian orders. Independent analysis of differential rates of karyotypic evolution in avian orders by Prager & Wilson (1980) is in agreement with my results. Whether rapid rate of chromosome change is correlated with extensive morphological change in passerines warrants further analysis.

Concluding remarks

My primary intent in this paper is to describe current methodologies and comparative results in the hope that others will be stimulated to conduct further avian cytogenetic research. Data available on bird chromosomes are truly meager. The large majority of studies are based on material taken from only one or several individuals and thus we know very little of the degree of intraspecific chromosome variation. Future research should include detailed comparative studies particularly between closely related species. The newly developed differential banding procedures will contribute greatly to more rigorous analysis at all levels. Finally, utilization of these techniques will provide further insight into the role of the avian chromosome in evolution, an area which has been greatly neglected.

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New Developments in Avian Systematics: A Summary of Results

K. H. Voous

What have been presented in this symposium are new developments in avian systematics, mainly in the neglected field of the systematics of higher categories. We have been confronted with new methods, new philosophies and new results.

New methods

Some of the new methods have been called the "molecular revolution" in biological research. But can we be sure that all new methods have been equally represented, or should amino-acid sequencing also have had to be included in this review, provided there are results from this field of research already available?

New philosophies

The following statements have emerged from this symposium and may better be seen as new philosophies than as conclusions or results: —

(1) Morphology is a better index to ecology than to phylogeny.

(2) Macromolecules and anatomical and behavioural features evolve at independent rates.

(3) Immunological differences are considered to be measurable as rates of protein evolution.

(4) Evolutionary change at the DNA level proceeds at a constant average rate over long spans of time.

(5) Avian chromosomal evolution is conservative.

These philosophies might suggest that results in the field of comparative ethology, greatly needed though they are, are informative only at the evolutionary level of species and perhaps genera. But is this true?

Non-ornithologists among systematists will have wondered why numerical taxonomy has not been included by the convenors in this symposium. I think the answer is clear: in spite of very clever attempts it has not yet led to any new results in ornithology and most of us wonder whether it will do so in the future.

Electron-microscopic comparison of tissues, carefully excecuted by e. g., Ziswiler in Zürich, though promising, is perhaps also too static for the approach presented here.

New results

Most striking, and for some of us even bewildering, are some of the detailed conclusions, the major ones of which can be listed as follows: —

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(1)The theory of the monophyletic origin of the Palaeognathae (Ratites and Tinamids) has been confirmed by quantitative immunological comparison of transferrin by Prager & Wilson.

(2) The close relationship of penguins and albatrosses and petrels has not only been confirmed by Prager & Wilson, but has also been supported by Jacob, based on preen gland secretions.

(3) Prager & Wilson found that gallinaceous birds and the duck-swan tribe share a remarkably isolated systematic place. Jacob found the same for each of these groups, but without any resemblance between the two.

(4) Quite unexpectedly, the systematic position of the flamingoes is still balanced between the Ciconiiformes and Anseriformes, as in contrast to most other recent findings Jacob found a great similarity of flamingoes with swans, geese and duck (also suggested by Mallophaga). But do perhaps feather waxes and feather lice respond, irrespective of the phylogeny of the birds, in similar ways to similar conditions of feathers and habitats?

(5) Prager & Wilson found the group of water birds to include both grebes and loons. In contrast to recent findings by Robert Storer, loons were as distant from the wader-gull-auk group as were grebes.

(6) Of all birds, owls were found by Prager & Wilson to resemble the water bird group. But Jacob found resemblances with "more likely" groups, such as cuckoos, woodpeckers and passerines. In both instances we have to ask what "resemblance" really means.

(7) The most highly branched wax molecule ever identified in preen gland secretions was found in *Alcedo atthis.* Provided the reasoning is not circular, this could mean that the branching off of the tyrannoid stock of passerines from the kingfishers in the sense of Feduccia would have taken place at a very early, if not too early a date. However, as the composition of preen gland secretions among the many and varied members of the group of kingfishers is largely unknown, such a conclusion would be premature at least.

(8) Among the passerines, Sibley & Ahlquist found chat-like thrushes, like the Robin-Nightingale complex, to be closely related to the muscicapids. This makes perfectly good sense, more particularly for the bright-coloured and sweet-singing eastern palaearctic flycatchers. But how to interpret the apparent similarity of the enigmatic Motacillidae and the Ploceidae, or of the Sturnidae and the Mimidae?

(9) Jacob found similarities in preen gland secretions in *Remiz, Panurus* and *Aegithalos,* and of these birds with Sylviidae, which sounds hopeful.

(10) Chromosomal variability between species of the same genus is greater in passerines than in other orders analyzed by Shields and his students. Therefore the close genetic resemblance between species of the North American emberizine genera *Zonotrichia* and *Junco* is the more remarkable and invites taxonomic action.

From the list of results given above it will be apparent that throughout the symposium, systematics and evolutionary history have been strongly inter-woven into an attempt to reach a synthesis. In none of these cases have Hennigian views on cladistic evolution prevailed. The reason for this may perhaps be found in the fact that although

detailed and sometimes exceedingly clever analyses (e. g., by CRACRAFT and FEDUCCIA) following HENNIGIAN methods have led to synthetic results, these have been constantly surrounded and severely threatened by the very same pitfalls in which half a century ago classical comparative anatomy foundered, where it has since remained dormant, if not dead. The HENNIGIAN practice in taxonomy easily leads to the reconstruction of phylogenies of organ systems and structures rather than of organisms. This aspect, dealt with on other occasions during this Congress, is certainly one of the dangers attending a conclusion like that of JACOB's that the Podicipediformes arose very early in the evolutionary process because of the complexity of their preen gland waxes. This conclusion sounds familiar. But how to avoid circular reasoning when it is equally stated that a phylogenetically young group like the Ploceidae has preen gland secretions of a simple composition, in this case mostly containing one wax? Nevertheless, all of JACOB's work seems to confirm the present, generally adopted system remarkably well.

On the other hand, can we be as revolutionary and at the same time as confident as CHARLES SIBLEY, who tends to feel that former systematic chaos has turned into relative clarity by the analysis of DNA differences? It is thrilling, but I am still hesitant. Though eager to accept well founded new ideas, I feel reluctant to discard all achievements by the classic anatomists like MAX FÜRBRINGER and HANS GADOW, though the slim basis of some of the 19th century anatomists' conjectures has been clearly exposed by SIBLEY & AHLQUIST in an earlier paper (Bull. Peabody Mus. Nat. Hist. 39 (1972) p. 5—28), and prefer to await the outcome of the present revolution. But I am hopeful only as long as we are modest enough to advance on the reliable, analytical and empirical road of all natural sciences and do not feel ashamed to continue to call the crow and the raven, like the mockingbird and the lark, songbirds—without having any exact knowledge of their places in evolutionary history. But, as SIBLEY remarked when reading this summary, "we can know — and do know, for some—and will know for others!" Such really is the battlefield, or should I say the communal workshop, of another session of the Congress—or of the next Congress.

In the meantime, cautious conservatives and bold revolutionaries alike should remember ALFRED NEWTON's words of more than a century ago:

"With regard to a systematic arrangement of birds, I am much mistaken if we are not on the verge of the adoption of changes which a short time ago would have astonished the most learned ornithologists . . . I must confess I think our results are likely to be lasting ones." (ALFRED NEWTON, February 12, 1867. Cited from A. F. R. WOLLASTON (1921) Life of ALFRED NEWTON. p. 214—215.)

SYMPOSIUM ON
RECENT ADVANCES IN AVIAN PALEONTOLOGY

6. VI. 1978

CONVENERS: J. A. FEDUCCIA AND S. L. OLSON

Martin, L. D.: Foot-Propelled Diving Birds of the Mesozoic 1237
Feduccia, A.: Evolution von Enten und Flamingos 1243

Foot-Propelled Diving Birds of the Mesozoic

Larry D. Martin

Introduction

The discovery of additional specimens of *Archaeopteryx* (Ostrom, 1973; 1974; 1975) has resulted in new interest in the Mesozoic toothed birds. After *Archaeopteryx* the best known and most important of these belong to an archaic group of diving birds, the Hesperornithiformes. Modern diving birds can be divided into two functional groups on the basis of how they propel themselves under water (Storer, 1958). One group, the wing-propelled diving birds, includes the diving alcids and penguins. No wing-propelled diving birds are presently known from the Mesozoic, and Eocene penguins from South America are the earliest known birds possessing this adaptation. Foot-propelled diving birds include loons, grebes, cormorants, and some anseriformes, as well as the extinct Hesperornithiformes.

The Hesperornithiformes range in age from Early to Late Cretaceous and geographically they occur in Europe, South America, and North America. They are nearly restricted to marine deposits and are the most common Mesozoic birds known. Because of this we can say a great deal about their anatomy and form a reasonable estimate of their phylogenetic affinities.

Origin of the Hesperornithiformes

While it is true that in their adaptations for foot-propelled diving, the hesperornithiform birds are among the most specialized of any of the Mesozoic birds, in most other respects they are only a little advanced over *Archaeopteryx*. The skull of *Hesperornis* has recently been redescribed by Gingerich (1972; 1976). who concluded that the palate was essentially palaeognathus and that the only kinesis present was a unique fore-aft movement of the maxillae which he called maxillokinesis. If his interpretation is correct, the common ancestor of *Hesperornis* and carinate birds lacked the prokinesis found in all modern carinate birds. The teeth of *Hesperornis* resemble closely the teeth of the other known toothed birds, *Ichthyornis* and *Archaeopteryx* (Martin & Stewart, 1977).

Ostrom (1976) has provided us with an excellent discussion of shoulder girdle and wing morphology of *Archaeopteryx* in relationship to the origin of powered flight in birds. I agree with Ostrom that *Archaeopteryx* lacked the capacity for "true" (sustained) powered flight. However, I am not convinced that the modifications of the wings and feathers in *Archaeopteryx* are for prey capture (Ostrom, 1974) rather than for an arboreal existence. Ostrom's arguments concerning the lack of powered flight in *Archaeopteryx* may be applied directly to the condition in the Hesperornithiformes. All known Hesperornithiformes are foot-propelled diving birds with heavy non-pneumatic skeletons. In fact the thick, dense bone in their skeletons is reminiscent of the pachyostosis of marine mammals and plesiosaurs. Their wings are extremely reduced

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and their sterna lack keels. Three genera, *Hesperornis, Baptornis,* and an undescribed hesperornithid (Martin, MS) have the wings and the shoulder girdles preserved, but the radius and ulna are only known in *Baptornis.* The carpals, metacarpals and phalanges are unknown for any hesperornithiform and were very small if present at all. In *Baptornis* the presence of at least carpals and probably metacarpals is indicated by the presence of distinct distal articulations on the radius and ulna. The condylus metacarpalis on the distal end of the ulna in *Baptornis* does not have the elongate form found in carinate birds (Martin & Tate, 1976), but rather resembles the condition in *Archaeopteryx* and dinosaurs (Ostrom, 1976). This suggests that the separation of *Baptornis* and the other hesperornithiform birds from the line leading to the carinate birds preceded the development of their characteristic fused carpometacarpus.

The humerus in the hesperornithiform birds is long and slender. In Baptornis the distal end is simple as it is in *Archaeopteryx* (Martin & Tate, 1976, Fig. 9), and lacks the distinct internal and external condyles found in all carinate birds including *Ichthyornis.*

Ostrom (1976) discusses a number of characteristics of the *Archaeopteryx* coracoid that were modified by carinate birds in order to make true powered flight possible. In *Archaeopteryx* the medial border of the coracoid is broad and the neck is not elongated giving a subquadrangular appearance. The scapula is fused to the coracoid and articulates above the brachial tuberosity. In *Hesperornis* the coracoid is also subquadrangular and the brachial tuberosity is at the same level as or slightly below the scapular facet, indicating a shoulder girdle only slightly advanced beyond the condition in *Archaeopteryx.* However, *Archaeopteryx* retains a series of primitive features: unossified sternum and sternal ribs, gastralia, amphicoelous vertebrae, elongate tail, and either the absence or lack of ossification of the uncinate processes on the ribs. Hesperornithiforms known from adequate specimens have ossified sterna that lack keels, sternal ribs, uncinate processes, and heterocoelous vertebrae. They lack gastralia and have shortened the tail in comparison to *Archaeopteryx.* The shortening of the tail is accomplished in *Hesperornis* by fusing some ten postacetabular vertebrae into the sacrum and two into the pygostyle. In *Baptornis* seven are fused into the sacrum and five into the pygostyle. This, coupled with the difference in shape of the caudal vertebrae and pygostyle between these two genera, suggests that their common ancestor had already begun to incorporate vertebrae into the sacrum but lacked a pygostyle with more than two fused vertebrae. All carinate birds fuse more than two vertebrae into the pygostyle.

In Hesperornithiform birds the clavicles are unfused and relatively weak contrasting with the large furcula found in *Archaeopteryx,* but they do not resemble closely the furcula of any carinate birds. The vertebrae of *Hesperornis* and *Baptornis* are fully heterocoelous contrasting with both *Archaeopteryx* and the earliest known carinate bird, *Ichthyornis.* In fact, *Hesperornis* is more advanced than most modern birds in having all the lumbar vertebra heterocoelous. *Ichthyornis* shows incipient heterocoely in its cervical vertebrae (Martin & Stewart, MS); the condition of the vertebrae in the earliest known hesperornithiform, *Enaliornis,* needs to be reexamined. At the present time I suspect that fully heterocoelous vertebrae were developed independently by hesperornithiform and carinate birds. Other derived features which unite hesperornithiform and carinate birds include the loss of the premaxillary teeth and the completion of tarsal fusions in the ankle joint.

Primitive features of the hesperornithiform birds which are shared with many other Mesozoic taxa include the absence of penetrating proximal foramina and the absence of a hypotarsus on the tarsometatarsus, and of a supratendinal bridge on the tarsometatarsus.

The common ancestor of carinate birds and the Hesperornithiformes was apparently a bird with the coracoid and wing only slightly more advanced than in *Archaeopteryx*, but with the first beginnings of heterocoelous vertebrae (as in *Ichthyornis)*. Sustained powered flight would probably not yet have been possible, and the Hesperornithiformes were beginning to utilize very different type of locomotion (foot-propelled diving) at about the same time as the perfection of powered flight was occurring in carinate birds. In other words, foot-propelled diving, light flight, was one of the basic adaptive zones into which birds radiated early in their history. Perhaps the early acquisition of endothermy and the insulative covering of feathers gave these early divers some advantage over small aquatic, ectothermic reptiles.

Diversity of the Hesperornithiformes

The earliest known hesperornithiform bird, *Enaliornis*, is Albian (Lower Cretaceous) in age and thus only slightly younger than *Archaeopteryx*. However, it already shows the enlargement of the cnemial crest on the tibia, shortening of the femur and compression of the tarsometatarsus characteristic of foot-propelled diving birds (STORER, 1958). In fact, it is at nearly the same level of adaptation as a loon and has been referred to the *Gaviiformes* by BRODKORB (1963). However, I would refer it to the Hesperornithiformes on the basis of the short triangular cnemial crest on the tibia (unlike loons the patella is important in hesperornithiform birds and the cnemial crest never becomes long and sharply pointed) and the presence of a distinct anterolateral ridge leading into the outer trochlea of the tarsometatarsus. No diagnostic gaviiform features are present. Apparently the fusion of the tarsals to the tibia was complete in the adult, but the only known proximal end of a tarsometatarsus is unfused and thus either this specimen was a young bird or the tarsometatarsus had not formed at this evolutionary stage. The vertebrae are reported to be heterocoelous (SEELEY, 1876) but require redescription.

The next record of the Hesperornithiformes is based on very complete material from the Niobrara Chalk (Santonian-Coniacian) of Kansas. Here the dominant genus is *Hesperornis*, and the most common species is *Hesperornis regalis*. This species may include *H. crassipes* and *H. gracilis* as large and small individual variations respectively. Besides *H. regalis*, there is a small unnamed species of *Hesperornis* and a new genus of hesperornithid. The Hesperornithidae are the best known of the Hesperornithiformes and are probably represented by material from more than one hundred individuals. They are the most highly evolved hesperornithiform birds with regard to foot-propelled diving and are the most specialized of any known birds for this type of locomotion. They share with grebes special articulations on the toes of the hind foot which permit them to be turned sideways on the recovery stroke; and it seems almost certain that, also like grebes, their toes were lobed (STOLPE, 1935). Although the other hesperornithiforms lack such a high degree of toe rotation, it would be reasonable to assume lobed rather than webbed feet for the order, and in fact *Baptornis* shows some indica-

tion of incipient toe rotation (Martin & Tate, 1976). The only known foot and feather impressions (Williston, 1898; Martin & Tate, 1976) show that the feet were scutellate-reticulate. A covering of feathers similar to that found on modern penguins would be a good guess as to the nature of the plumage.

The outer toe is much enlarged in *Hesperornis* and the tibia is elongate, and lies closely parallel to the ilium. As Heilman (1927) has pointed out, it would be impossible for *Hesperornis* to rotate its legs under its center of gravity, and the legs were permanently fixed to the posterior end of the body. *Hesperornis* must have progressed on land by pushing itself on its belly with its hind feet, much like a seal; but, unlike a seal, the neck was elongate and the whole body was long and slender. *Hesperornis regalis* was about five feet in length and there is at least one smaller species of *Hesperornis* and a related genus of intermediate size in the Niobrara Chalk. In the overlying Pierre Shale (Campanian) we have a *Hesperornis* which is the size of *H. regalis* and three smaller, undescribed species including one the size of a large grebe. I am presently maintaining *Coniornis* from the Claggett Formation of Montana as a valid genus and I follow Brodkorb (1963, p. 192) in treating *Hesperornis montana* Shufeldt (1915) as a junior synomym of *Coniornis altus* Marsh (1893).

The Baptornithidae includes hesperornithiform birds lacking well-developed toe rotation and having somewhat less reduced wings. The caudal vertebrae of the baptornithids also lack the broad, flat transverse processes and fused intercentra that give the caudals of the hesperornithids their characteristic form. The patella in *Baptornis* is centered on the tibia and lies between the condyles of the femur. In *Hesperornis* the patella articulates with the anterior face of the outer condyle of the femur. This is similar to the situation found in grebes, but in both *Hesperornis* and *Baptornis* the patella contains a foramen for the ambiens muscle which is lacking in the Podicipediformes. A small undescribed genus occurs with *Baptornis* in the Niobrara Chalk and *Neogaeornis* from the late Cretaceous of Chile is also included in the Baptornithidae (Martin & Tate, 1976). *Baptornis* is the only Mesozoic bird for which early juveniles can be identified (Martin & Bonner, 1976), and these specimens raise questions about the location of nesting sites. Thus far, almost all evidence points to the Hesperornithiformes as being exclusively marine, although Fox (1974) has reported a specimen of *Hesperornis* from an estuarine deposit. The only likely exception is an undescribed diving bird from dinosaur-bearing sediments in South Dakota. It seems likely that the Hesperornithiformes nested in rookeries on isolated coastlines, or perhaps on off-shore islands as do many modern birds. The existence of such a rookery has been suggested by Russell (1967) but his birds are not immature enough to support his case strongly.

We now have at least seven genera and thirteen species of hesperornithiform birds ranging in age from Albian (Early Cretaceous) to Campanian (Late Cretaceous). Of these, six species and two genera are presently undescribed (Martin, MS). Besides this, new material from the Maestrichtian of South Dakota (Martin, MS) suggests the existence of an undescribed, nonmarine subfamily of hesperornithiform birds.

Affinities of the Hesperornithiformes

Mars allied *Hesperornis* with the ratites on the basis of its flat sternum and palaeognathus palate. In fact, he characterized it as "essentially a carnivorous, swimming

ostrich" (Marsh, 1880: 114). This does not mean that Marsh was unaware of the many similarities between *Hesperornis* and the modern foot-propelled diving birds. He used the loon and grebe as the standard of comparison throughout his work, but regarded their similarities with *Hesperornis* as convergence. D'Arcy Thompson (1890); Lucas (1903), Shufeldt (1915) and Heilman (1927) all pointed out differences between Hesperornis and living ratites and stressed the similarities with loons and the Podicipediformes. However, most authors (Wetmore, 1956; Brodkorb, 1963) have regarded the hesperornithiformes as a primitive sidebranch of avian evolution. This treatment has been abundantly supported by my recent studies. The primitive nature of the shoulder girdle, wings, and tail of the hesperornithiform birds demonstrated that any common ancestor between them and the carinate birds lacked the capacity for sustained slight and all carinate birds are more closely related to each other than any is to the Hesperornithiformes.

In other words, the foot-propelled diving birds of the Mesozoic are not the progenitors of any modern group of diving birds, but are instead a sister group of all carinate birds. They are an early avian experiment which developed in parallel to the evolution of powered flight and was extremely successful as is demonstrated by their wide geographic distribution, high diversity, and long geologic range. This experiment was terminated at the end of the Cretaceous by the same wave of extinction that claimed the dinosaurs. Foot-propelled diving birds do not appear again until the advent of loons and grebes in the middle of the Cenozoic.

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Evolution von Enten und Flamingos

Alan Feduccia

Einleitung

Vögel, so wird unter Zoologen allgemein gesagt, sind die am besten erforschte Gruppe der heute lebenden Wirbeltiere, und im großen und ganzen ist das auch richtig. Charles Darwins Werk „Über die Entstehung der Arten durch natürliche Zuchtwahl" beruhte zu einem großen Teil auf Beobachtungen, die er an Haustauben und Galapagos-Finken (oder Darwin-Finken) gemacht hatte. Vor allem diese Finkenpopulationen, die auf jeder Insel des Galapagos-Archipels Variationen zeigten, führten ihm die Wandlungsfähigkeit der Lebewesen deutlich vor Augen.

Doch obwohl Vögel besser erforscht sind als andere Wirbeltiere, so ist über die Verwandtschaftsbeziehungen zwischen den höheren Vogelkategorien nur wenig bekannt. Diese Lücke in unserem Wissen hat eine ganze Reihe wichtiger Gründe. Der erste und wohl wichtigste Grund ist die morphologische Gleichförmigkeit der Vögel. Sie wird zweifellos bedingt durch Anforderungen, die das Fliegen an den Körperbau stellt. Um sich dies zu verdeutlichen, braucht man nur zu bedenken, wie viele Möglichkeiten ein Ingenieur beim Bau eines Landfahrzeuges hat. Für ein Luftfahrzeug mit Flügelantrieb gibt es jedoch nur einen grundlegenden Konstruktionsplan. Die physikalischen Anforderungen des Fliegens sind also die Ursache dafür, daß sich alle Vögel unter ihren Federn sehr ähnlich sind. Während es bei den Säugetieren z. B. eine Vielzahl von Eigenschaften gibt, die die einzelnen Gruppen voneinander unterscheiden (wie die Zähne), gibt es bei den höheren Kategorien der Vögel sehr wenig, was uns Hinweise auf ihre Verwandtschaftsbeziehungen geben könnte.

Ein weiteres Problem ist der Mangel an Fossilien. Als Anpassung an die Fortbewegungsart des Fliegens sind Vogelknochen sehr leicht und oft hohl. Deshalb, und da die meisten Vögel auf Bäumen leben, sind ihre Knochen als Fossilien nicht sehr gut erhalten. So ist es verständlich, warum zusammengehörige Knochenfunde fossiler Vögel für die Wissenschaft so wichtig sind, denn sie helfen, die stammesgeschichtlichen Zusammenhänge zwischen heute lebenden Vogelordnungen zu erklären. Während wir die meisten Wirbeltiergruppen bereits seit langem durch zahlreiche fossile „missing links" miteinander verknüpfen können, fehlte es bei den Vögeln bisher noch an den notwendigen Belegfossilien (Feduccia, 1976, 1977a, b). In diesem Artikel nun möchte ich die Entdeckung von erstaunlich großen Ansammlungen von Fossilien eines flamingoähnlichen Watvogels beschreiben, der aus dem Eozän vor 50 Millionen Jahren stammt.

Presbyornis: Der rätselhafte Vogel

Die Fundstätte dieses Vogelfossils liegt in der sogenannten Green-River-Formation, die sich vom Südwesten des US-Staates Wyoming bis in den Südosten des Staates Utah erstreckt. Für Zoologen ist dieses Gebiet eine regelrechte Schatzkammer an evolutionsgeschichtlich wichtigen Fossilien des Eozäns. Von besonderer Bedeutung sind hierbei Funde von Vogelknochen, die vor kurzem gemacht worden sind. Sie lagen alle in den

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Schichten des frühen Eozäns (jedoch der späten Wasatch-Stufe), was darauf hinzudeuten scheint, daß sie wohl aus der späten Periode des frühen Eozäns stammen. In letzter Zeit wurden hier nun auch enorme Mengen von Vogelfossilien entdeckt, die alle einer einzigen Spezies angehören. Diese Forschungsarbeiten wurden vor allem von Studenten und Arbeitsgruppen unter Leitung von Paul O. McGrew (McGrew & Feduccia, 1973; Feduccia & McGrew, 1974) von der Universität Wyoming geleistet und teilweise von der National Geographic Society mit unterstützt.

Ich hatte die Möglichkeit, diese Fossilien eingehend studieren zu können. Sie sind so besonders interessant, weil es sich hier um fast vollständige Fossilien einer einzigen Spezies handelt, nämlich des *Presbyornis pervetus*. Alexander Wetmore (1926), der führende amerikanische Ornithologe und frühere Vorsitzende der Smithsonian Institution in Washington, hatte ihn bereits 1926 als neue Familie (Presbyornithidae), Genus und Spezies eines Strandvogels, beschrieben. Die Entdeckung fast vollständiger *Presbyornis*-Skelette öffnet nun das Tor zu einer totalen Neubewertung der Verwandtschaften zwischen einer Anzahl heute lebender Vogelordnungen. *Presbyornis* ist nämlich ein seltsames Evolutionsmosaik, eine Art Montage der morphologischen Merkmale von Strandvögeln (Charadriiformes), von heute lebenden Enten- und Gänsevögeln (Anseriformes) und heutigen Flamingos (Phoenicopteriformes).

Presbyornis: Ein zeitliches Relikt

Die Existenz von Flamingos oder flamingoähnlichen Vögeln läßt sich bis weit in die Kreidezeit zurückverfolgen, obwohl die Identität vieler Fossilien noch ziemlich ungewiß ist. Je weiter man in der Zeit zurückgeht, desto mehr ähneln sie nämlich den Strandvögeln; und wenn man nur einzelne Knochen zur Verfügung hat, ist es unmöglich, eine exakte und haltbare Rekonstruktion des gesamten Lebewesens vorzunehmen.

Auch die Identifizierung der ersten Ente aus dem Eozän Nordamerikas ist ungewiß, da sie sich nur auf ein ziemlich unzuverlässiges Fossil stützt, nämlich ein paar Flügelknochen. Die ersten zuverlässigen Entenfossilien stammen erst aus dem Oligozän. Da Enten mit großer Wahrscheinlichkeit als Fossilien konserviert wären, wenn es sie gegeben hätte (im nordamerikanischen Pliozän und Pleistozän findet man ihre Fossilien häufiger als die aller anderen Vögel), könnte man aus der Abwesenheit von Entenfossilien im frühen Tertiär schließen, daß Enten und ähnliche Vogelarten erst im mittleren Tertiär auftraten.

Presbyornis führt uns die Schwierigkeiten deutlich vor Augen, mit denen man bei der Interpretation früher tertiärer Fossilien konfrontiert wird. Nur nach dem (von Wetmore 1926 beschriebenen) Tarsometatarsus zu urteilen, handelt es sich bei *Presbyornis* mit Sicherheit um einen Strandvogel; und wenn man jetzt nur seinen Schnabel besäße, würde man ihn gewiß als „reine" Ente deuten. Es ist durchaus möglich, daß die meisten der Vogelfossilien des frühen Tertiärs bis zu einem gewissen Grad wie Mosaike sind, und deshalb ist man sicher gut beraten, der gesamten fossilen Belegreihe von Vögeln des frühen Tertiärs, die sich auf einzelne unzusammenhängende Skeletteile stützt, skeptisch zu begegnen. Wir können von Glück sagen, daß wir für *Presbyornis* tatsächlich zusammengehörende Knochenfossilien gefunden haben. Wenn nicht, würden wir diesen einen Vogel je nach dem Knochen, den wir gerade zur Interpretation zur Hand nähmen, als zu drei verschiedenen Arten gehörig klassifizieren: als Strandvogel, als Ente oder als Flamingo.

Man darf auf keinen Fall versucht sein, in der fossilen Belegreihe nach Vorfahren heute lebender Arten zu suchen, denn kein Lebewesen kann nur „Vorfahr" ohne spezielle Adaptationen an seine besondere Umwelt sein. Es gibt jedoch eine Vielzahl von Wirbeltierfossilien, die eine Lücke zwischen verschiedenen Gruppen sehr gut überbrükken, obwohl sie selbst irgendwie für eine bestimmte Lebensform spezialisiert sind. Wir haben z. B. hinlänglich gute Übergangsfossilien zwischen dem Quastenflosser *Rhipidistia* und den ersten Amphibien, den Panzerlurchen, zwischen Amphibien und Reptilien, Reptilien und Vögeln sowie Reptilien und Säugetieren. Es ist besonders interessant, hier *Presbyornis* mit dem Anthracosaurier *Seymouria* zu vergleichen, denn dieser ist zwar ein perfektes morphologisches Zwischenglied zwischen Amphibien und Reptilien, doch tritt *Seymouria* erst in der Permzeit auf, während der Übergang von Amphibien zu Reptilien bereits in der Karbonzeit, also bereits Millionen Jahre früher, stattgefunden hatte. Genauso zeigt *Presbyornis* viele der morphologischen Züge, die man leicht mit den Vorfahren der heute lebenden Enten und vielleicht sogar mit den heutigen Flamingos in Verbindung bringen könnte. *Presbyornis* tritt jedoch erst im Eozän auf, also wahrscheinlich später, als die eigentlichen Übergänge wirklich stattgefunden hatten; da er ein zeitliches Relikt ist, und obwohl viele seiner Züge spezialisiert sind, zeigt er immer noch viele morphologische Merkmale, die darauf hindeuten, daß es sich bei ihm um einen gemeinsamen Vorfahren von Enten und Flamingos handelt. Aus diesem Grund lohnt es, eine Hypothese der Entwicklungsstadien zu diskutieren, die Enten und Flamingos durchlaufen haben könnten.

Entwicklungsstadien von Enten und Flamingos

Während der letzten hundert Jahre sind 15 verschiedene Klassifikationen entwickelt worden, in denen Flamingos in die Nachbarschaft von Störchen, Ibissen und Reihern (Ciconiiformes) oder von Enten und ähnlichen Arten (Anseriformes) gerückt wurden. Die Herkunft der Enten war bisher ein vollständiges Rätsel. Nach der Wiederentdekkung von *Presbyornis* wissen wir jetzt, daß sowohl flamingoähnliche als auch entenartige Vögel von den Strandvögeln abstammen, und daß die Ciconiiformes wenig, wenn überhaupt etwas mit Flamingos oder Enten zu tun haben; ihre Ähnlichkeit mit den Flamingos (vor allem ihre langen Watbeine) ist ganz oberflächlich und beruht auf konvergierenden Entwicklungen, die sich aus ähnlichen Umweltbedingungen ergaben. Sogar die verschiedenen Gruppen der Ciconiiformes sind nicht eng miteinander verwandt, und man weiß mit Sicherheit, daß Reiher weder mit Störchen noch mit Ibissen viel gemein haben. Mit Hilfe des Evolutionsmosaiks *Presbyornis* jedoch können wir die hypothetischen Stadien rekonstruieren, die die heutigen Enten und Flamingos bei ihrer Evolution durchlaufen haben könnten.

Wie bereits gesagt, soll man *Presbyornis* nicht als echten Vorfahren, sondern als zeitliches Relikt ansehen, das lange nach der Entstehungszeit der neuen Ordnungen auftrat, wie es z. B. auch beim Anthracosaurier *Seymouria* der Fall war. Sowohl *Seymouria* als auch *Presbyornis* sind in gewissen Graden spezialisiert, und doch würde eine *Presbyornis*-ähnliche Form viele der morphologischen Merkmale aufweisen, die für einen gemeinsamen Vorfahren sowohl der heutigen Enten als auch der Flamingos erforderlich wären.

Man könnte sich den Ablauf der hypothetischen Entwicklungsstufen etwa folgendermaßen denken: *Presbyornis* gehört offensichtlich zu den Phoenicopteriformes, einer

Ordnung, zu der auch die heutigen Flamingos zählen, doch besitzt er andererseits so viele morphologische Züge, die Zwischenformen zwischen Flamingos und Strandvögeln darstellen, daß man nicht länger daran zweifeln kann, daß die flamingoähnlichen Vögel in der Tat von den Strandvögeln abstammen. Silhouette A der Abb. 1 stellt einen solchen Strandvogel-Vorfahren dar, wie er höchstwahrscheinlich in der späten Kreidezeit existiert hat. Solch ein Stamm hat all die morphologischen Züge, die ihn als Vorfahren einer Vielzahl von flamingoähnlichen Vögeln qualifizieren, wie wir sie aus fossilen Belegen des Tertiärs kennen, und die auch solche Formen wie *Presbyornis* oder *Presbyornis*-ähnliche Vögel umfassen. Darüber hinaus haben wir geologische Beweise dafür, daß *Presbyornis* genauso wie der heutige Flamingo an salzhaltigen Seen mit großen Algenfeldern lebte. Man darf deshalb mit Sicherheit annehmen, daß *Presbyornis'*

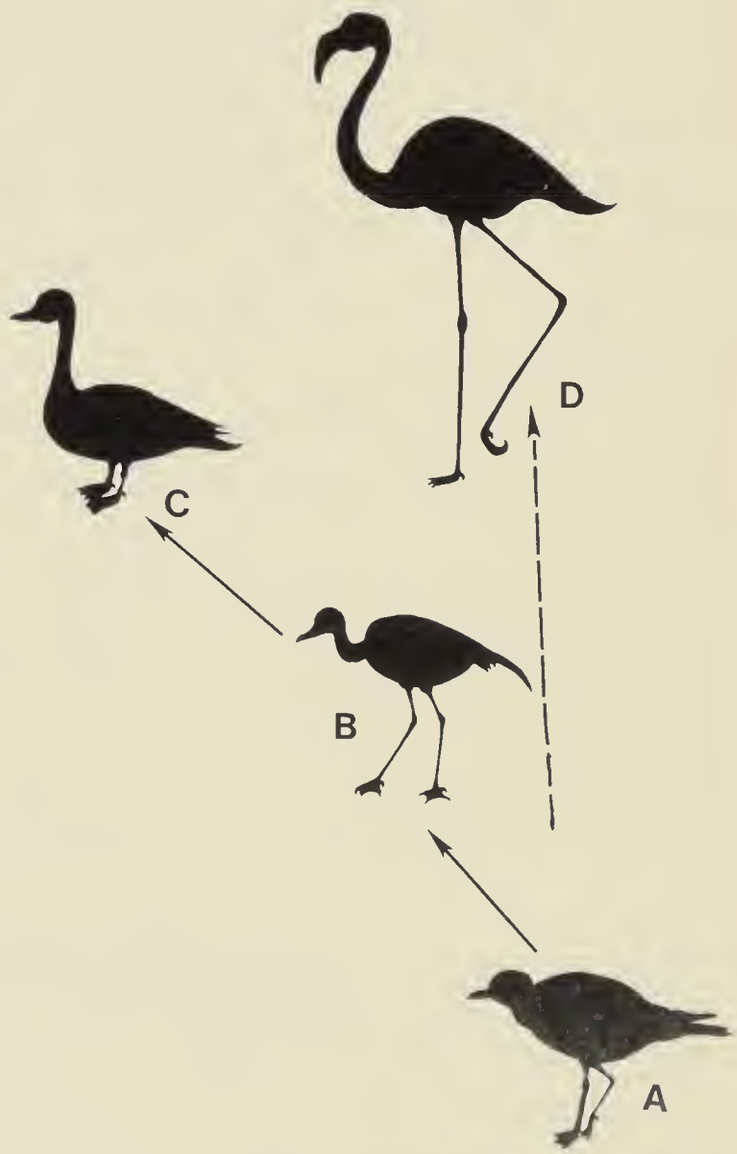

Abb. 1. Eine hypothetische Phylogenie, die den wahrscheinlichen Entwicklungsablauf von Enten und Flamingos darstellt. (A) stellt einen Stamm von Strandvogelvorfahren aus der Kreidezeit dar. Sie sind mit großer Wahrscheinlichkeit die Vorläufer der flamingoähnlichen Vögel, die durch viele verschiedene Seitenlinien vertreten sind; eine von ihnen ist das Evolutionsmosaik *Presbyornis,* das Merkmale der Strandvögel, Enten und Flamingos aufzeigt. *Presbyornis* (B) vereint vor allem ein für Strandvögel und Flamingos typisches Körperskelett mit einem entenartigen Schädel (und dem für Flamingos typischen Gelenk zwischen Stirnbein und Oberschnabel). Eine Form, die *Presbyornis* in vielen seiner morphologischen Merkmale nahekommt, könnte ein denkbarer Vorläufer (vielleicht jedoch kein tatsächlicher Vorfahr) sowohl der heutigen Enten als auch der Flamingos sein. *Presbyornis* selbst ist mit Sicherheit ein in gewissen Hinsichten spezialisiertes zeitliches Relikt. Die Linie, die zu den heutigen Flamingos führt (D), würde von einem *Presbyornis*-ähnlichen Vorfahren fordern, daß sich sein Schnabel so weitgehend modifiziert, daß er seine Nahrung aus dem Wasser herausfiltern kann (Biegung des Schnabels etc.) und daß sich seine Beine zum Waten in tieferem Wasser erheblich verlängern. Die gestrichelte Linie zeigt, daß unsere heutigen Flamingos zweifellos lange vor *Presbyornis* entstanden waren, vielleicht jedoch von einem morphologisch ähnlichen Vorfahren abstammen. Auf dem Wege, der zu den Enten führt (C), verkürzen sich die Beine für besseres Schwimmvermögen, aber der Schädel bleibt im großen und ganzen derselbe wie bei *Presbyornis* (abgesehen von einigen Veränderungen der Schnabelgegend). (Feduccia, 1977b.)

Umwelt und seine Lebensgewohnheiten im großen und ganzen denen unserer heutigen Flamingos recht ähnlich gewesen sein können. Wahrscheinlich hat *Presbyornis* bei der Futtersuche Algen aus dem Wasser gefiltert, obwohl seine entenartige Schnabelform sicher auch andere Futteraufnahme zuließ, und er vielleicht noch zusätzlich eine Vielzahl anderer Organismen fraß. Auch unsere heutigen Flamingos fressen natürlich zusätzlich zu den Algen noch eine ganze Anzahl kleiner aquatischer Lebewesen.

Wenn nun eine Form wie *Presbyornis* oder *Prae-Presbyornis* an diesen großen salzhaltigen Seen des Eozäns auftaucht, ist es leicht vorstellbar, daß eine starke Selektion zugunsten der Entwicklung von langen Beinen stattfindet, die zum Waten in tiefem Wasser besonders gut geeignet sind. Gleichzeitig würde sich auch eine Vielzahl anderer Modifikationen ergeben, wie z. B. die des Schnabels zur Vervollkommnung eines Saugfiltermechanismus. Hier sei daran erinnert, daß die heutigen Flamingos als Junge einen geraden Schnabel haben. Unter Beibehaltung der ursprünglichen Umwelt und mit relativ geringfügigen morphologischen Veränderungen kann man sich leicht die Entwicklungsstufen vorstellen, die zum Flamingo führen, wie wir ihn heute kennen (D).

Weiter erscheint es nicht zu gewagt, sich eine Reihe von Entwicklungsstufen vorzustellen, die von einem *Presbyornis*-ähnlichen Vorfahren zu den heutigen Enten und ähnlichen Arten geführt haben mögen. *Presbyornis* hatte bereits einen entenartigen Schnabel (eine Anzahl heutiger Enten filtert ihre Nahrung auch aus dem Wasser heraus), und nur mit geringfügigen Modifikationen könnte sich sein Schnabel zu dem der heutigen Entenvögel umgeformt haben. Darüber hinaus würde eine Verkürzung der Beine, die dann auch eine Veränderung des Knochengerüstes mit sich brächte, ihr Schwimmvermögen verbessern. Man könnte sich eine Situation denken, in der ein See z. B. nur einen schmalen Uferstreifen besitzt. In diesem Falle wäre es für einen *Presbyornis*-ähnlichen Vogel vorteilhaft, in seiner Evolution sein Schwimmvermögen zu verbessern. Solche Veränderungen würden dann zum Prototyp der Enten führen, wie er in (C) dargestellt ist. All die verschiedenen Enten, Gänse und Schwäne, die einen so wichtigen Teil der heutigen Vogelwelt ausmachen, wären so auf die Wechselfälle der Evolution zurückzuführen, durch die der Schnabel so verändert wurde, daß er für eine Vielzahl verschiedener Lebensgebiete und Nahrungsquellen geeignet war.

Summary

Evolution of modern ducks and flamingos

A classical problem in avian systematics has been the phylogenetic relationships of the flamingos (Phoenicopteriformes). To date the generally held view has been that flamingos are either allied with the storks, ibises and herons (Ciconiiformes), or either the ducks, geese and swans (Anseriformes).

The rediscovery of an Eocene fossil *Presbyornis* (family Presbyornithidae) in unusually large concentrations with associated skeletons, has permitted a complete reassessment of the phylogenetic relationships of the Phoenicopteriformes. *Presbyornis* was originally described by Wetmore in 1926 as a new family of recurvirostrid shorebird on the basis of primarily the tarsometatarsus. However, with complete skeletons, it is now shown to be an Eocene flamingo-like wader. Indeed, *Presbyornis* is an evolutionary mosaic, combining characters primarily of the Charadriiformes and Anseriformes with some characters of living flamingos. It thus represents the first avian fossil to link a number of modern avian orders.

The skull of *Presbyornis* is extremely similar to that of living ducks but with a slightly recurved, ducklike bill, even with the nail in the tip. The nasal bones, however, form a V-shaped structure that is nearly identical to that of a 30-day old chick of the living flamingo, *Phoenicopterus ruber.* The postcranial skeleton exhibits a strange mosaic of primarily anseriform and charadriiform characters; in fact, the tarsometatarsus is essentially that of a shorebird, thus vindicating Wetmore. In addition, the humerus is very similar to living recurvirostrids and burhinids and Cretaceous shorebirds. The English reader is referred to a similar article by the author (Feduccia, 1978).

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SYMPOSIUM ON SPECIATION IN SOUTH AMERICAN BIRDS

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Avian Speciation Patterns in Upper Amazonia

Jürgen Haffer

Distribution patterns

Over half of the bird species inhabiting forests and forest borders in upper Amazonia occupy large portions or all of this region (60 % of a sample of 284 species). Many of them inhabit, in addition, all or part of eastern Amazonia. Several other species are mainly eastern Amazonian in distribution and range westward into parts of upper Amazonia. Some of the upper Amazonian species occur mainly in the hilly areas near the base of the Andes and range, north and south of the Marañón River, for varying distances east into the level lowlands. Almost 40 % (i.e. 112 species) of the forest birds range mainly to the north or to the south of the upper Amazon River occupying rather restricted areas. Among these species are many systematically isolated species or monotypic genera. In other cases, the northern and southern populations are representatives of an endemic upper Amazonian or more widespread species or superspecies. These representatives are separated by a distributional gap or they meet along a contact zone.

It is of interest to note that the distribution patterns of the upper Amazonian herpetofauna are similar to those of birds. Among the 185 species of amphibians and reptiles that Duellman (1978) reported from Santa Cecilia, eastern Ecuador, 84 species (45 %) are widespread in Amazonia and in part also occur in the lowlands west of the Andes. 87 species (47 %) are restricted to upper Amazonia, 23 of which are confined to eastern Ecuador and adjacent Colombia.

Secondary contact zones

The northern and southern representatives of 8 to 12 subspecies and species pairs of western Amazonian birds meet along portions of the upper Amazon River where the allies occupy opposite banks for varying distances. In 13 pairs the contact zones are located in continuous forests of the level upper Amazonian lowlands and no correlation with environmental features exists, such as river courses or hilly ranges. Further east, approaching the Rio Negro and the Rio Madeira, additional contact zones exist between western and eastern Amazonian allies which remain outside the present discussion.

The allied taxa, which come in direct contact, form (a) a hybrid zone of varying width, (b) a zone of overlap and hybridization or (c) they replace each other geographically in continuous forest habitat without or nearly without hybridization (parapatry); see Haffer (1974) for discussion of examples.

Distribution centers

In an attempt to illustrate distributional 'core areas' for the upper Amazon bird fauna, I superimposed the range outline maps of the members of northern and south-

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ern species groups in upper Amazonia regardless of whether these forms are taxonomically isolated species or close allies of some other Amazonian species. The resulting contour maps (Fig. 1) illustrate the number of species in these two distributional groups present in any given area (see HAFFER, 1978, for details of constructing these and other maps concerning distributional aspects of the Amazon forest bird fauna). Nearly all regionally restricted species of upper Amazonia cluster in two fairly small areas: in eastern Ecuador ('Napo center') and in southeastern Peru ('Inambari center'). Relatively few of the Ecuadorian species considered ('Napo forest birds') have entered southern Venezuela and few have crossed the Marañón-Solimões River southward.

FIGURE 1. Avian distribution centers in upper Amazonia. Contour lines indicate numbers of southern and northern endemic species and subspecies. Left: Inambari center; superimposed ranges of 47 species and subspecies. Right: Napo center; superimposed ranges of 38 species and subspecies of birds (after HAFFER, 1978).

This river probably acted as an effective barrier to dispersal for these species. In the eastern Peruvian subspecies and species considered ('Inambari forest birds'), a conspicuous gradient of decreasing total number of species within this group parallels the main rivers in this region which flow in a northern and northeastern direction (Rio Jurua, Rio Purus). 8 to 13 species of this group reached the southern bank of the Rio Solimões without crossing this river except for *Galbula cyanescens, Odontophorus stellatus,* and *Rhegmatorhina melanosticta* which followed the base of the Andes northward. The Rio Madeira blocked the eastward advance of many species and only four of the 'Inambari forest birds' managed to cross it.

The total number of bird species present between avian 'distribution centers' in Amazonia is more or less compensated for by species from a neighboring cluster and by species with extensive ranges. Only the 'Napo center' and, more weakly, the 'Guiana center' in northeastern Amazonia stand out as species-rich "peaks" on a distribution map of the pooled samples of Amazon forest birds (HAFFER 1978).

Discussion

Composite distribution maps provide quantitative data on avian core areas and on the location of secondary contact zones in upper Amazonia. The gradients of decreas-

ing species numbers around Amazonian 'distribution centers' may be due to decreasing dispersal distance of the various species in a given distributional group from a center of survival or origin (possibly combined with a correspondingly increased competitive pressure from other bird species) or due to decreasing resource levels in connection with changing ecological conditions in the forests themselves. The former interpretation is preferred for the majority of the species involved mainly because the secondary contact zones of birds (with or without hybridization) are located predominantly between distribution centers and geoscience data indicate the occurrence in Amazonia of Quaternary climatic-vegetational fluctuations (see SIMPSON & HAFFER, 1978, for a recent review).

Most of the bird populations in secondary contact along the Marañón-Solimões River as well as in the lowlands to the north and south of this river presumably have spread from eastern Ecuador (Napo center) and southeastern Peru (Inambari center), respectively. Portions of these areas probably served as 'refugia' for the forest biota during adverse climatic periods of the Quaternary (HAFFER, 1969, 1974). In these refugia, restricted populations of plants and animals (a) became extinct, (b) survived without much change or (c) differentiated to the level of new subspecies or species. Many forest birds are characterized by a high rate of differentiation under conditions of interrupted gene flow.

Direct evidence for the continued existence of forests in regions designated as Quaternary forest refugia does not (yet) exist. However, scattered geomorphological and palynological data from the central and eastern parts of Amazonia indicate repeated Pleistocene changes in the distribution of forest and nonforest vegetation to have taken place which, by implication, must have affected also upper Amazonia. The same is indicated by the results of GARNER's (1959) geomorphological work along the Amazonian slopes of the eastern Andes in Peru where climatic changes occurred during the Pleistocene. Sea-level fluctuations led to extensive environmental changes in Amazonia where, especially during early Pleistocene periods of raised sea-level (interglacials), huge inland lakes developed in the Amazon and Solimões Valley (IRION 1976).

Geological indications of environmental changes in upper Amazonia suggest that the parapatric and hybridizing allies in these regions are indeed in secondary contact. This interpretation contrasts to ENDLER (1977) who suggested on the basis of genetic considerations that the so-called 'contact zones' of members of the Amazon fauna might have developed in response to sharp environmental gradients without habitat or range fragmentation. However, no proof exists for the presence in Amazonia of sharp, linear, ecological gradients along the numerous contact zones of birds, plants and insects scattered over large areas of forest covered lowlands (SIMPSON & HAFFER 1978).

As to the high frequency of parapatric species in Amazonia, we may speculate that fairly rapid morphologic-behavioral differentiation of avian refuge populations occurred under conditions of reduced population size and interrupted gene flow. At the same time, the ecological requirements of the refuge populations may have remained rather unchanged presumably because ecological conditions in the forest refugia remained similar to those existing in the original continuous habitat. The local environmental conditions in the refugia probably were more or less constant through time, thereby possibly slowing the ecological deviation of many avian populations iso-

lated in the forest refugia. Presumably, parapatric species acquired reproductive isolation without having reached ecologic compatibility; each partner is competitively superior in the area occupied. Although Mayr (1951, 1969) and Vaurie (1955) have pointed out the existence of continental superspercies of birds, parapatric (i.e. nonhybridizing) allospecies have not been studied in detail along the contact zones. Diamond (1972) and Terborgh (1971, 1975) discovered competitive exclusion between pairs and sets of three or more congeneric species along altitudinal gradients of tropical mountains in New Guinea and eastern Peru, respectively. Among higher latitude birds, Selander & Giller (1959) and Ferry & Deschaintre (1974) studied pairs of parapatric woodpeckers and warblers, respectively. In all these cases, hybridization is absent or nearly absent. However, details of competitive interactions and of isolating mechanisms remain unknown. The North American species of *Passerina* and *Pheucticus* as well as other species pairs form rather extensive 'zones of overlap and hybridization' and, for this reason, remain outside our discussion of contact zones of nonhybridizing allospecies.

Parapatric bird species are fairly common, more so in low Latitude than in temperate zone avifaunas. Up to 60—80 % of the members of certain tropical families are allospecies of superspecies (many of which are in contact): African Laniidae 69.4 %, Timaliinae 64.5 %, Nectariniidae 67.6 % (Hall & Moreau 1970), Cracidae 75 %, Ramphastidae 85 %, Galbulidae 75 % (Haffer 1974), Pipridae 75 % (Snow 1975). Similarly high percentage figures probably will be obtained also for some bird families inhabiting lowland forest of tropical Asia. Unanswered questions in all these cases include "Which mechanisms assure reproductive isolation of competing species?", "Are parapatric species prevented from overlapping their ranges through behavioral responses or through resource preemption by the respective partners?", "Is the location of the contact zone determined mainly by historical or by extant ecological factors?", "What are the reasons that parapatric species do not penetrate the representative's range maintaining interspecific territories or occupying mutually exclusive patchy areas of varying size?" The latter situation may exist in cases of 'checkerboard allopatry' as discussed for New Guinea forest birds by Diamond (1972, 1973). A detailed field study of parapatric species pairs along their contact zones would contribute significantly toward a discussion of ecological aspects of the speciation process and of tropical species diversity.

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Speciation in Birds of the High Andes

François Vuilleumier

Introduction

Inspired by Chapman's writings but guided by Mayr's geographic speciation theory, I analyze speciation in birds inhabiting Andean páramo, puna, ceja, and montane steppe vegetation, describing a series of examples that bear on these questions: What ecological and geographical circumstances favor speciation today? and: Can speciation be correlated with environmental changes of the Pleistocene?

Methods and material

Assumptions

I assume that speciation is allopatric, and that the analysis of three phenomena (Mayr, 1963) permits one to deduce the conditions under which it occurs today:

(1) Geographical isolation (a) within species, and (b) between semispecies and allospecies (Amadon, 1966).

(2) Secondary contacts between former isolates.

(3) Broad range overlaps between closely related congeners.

To obtain data one assesses phylogenetic relationships among species, maps their distributions, and documents the nature of isolation or sympatry among taxa of a given genus.

High Andean vegetation and avifauna

Páramo is wet alpine-like, grassy or scrubby, *Espeletia*-dominated vegetation above timberline in Venezuela, Colombia, and Ecuador. Puna is drier, more open alpine-like vegetation in Perú, western Bolivia, northern Chile and northwestern Argentina, south to about 28° S. Ceja is wet forest and bushy vegetation from 2000—2500 m up to timberline from Venezuela and Colombia southward to northwestern Argentina at about 28° S. Montane steppe is xeric, savanna- or steppe-like vegetation from 1500—2000 m up to timberline from Venezuela and Colombia southward to northwestern Argentina at about 28° S, and occurs on Andean slopes or the floor and slopes of montane basins.

I assign about 144 land bird species and semispecies to the páramo-puna, 512 to the ceja, and 336 to the montane steppe faunas, respectively. The combined páramo-puna and ceja faunas include about 649 species (25 % of all South American species); the combined páramo-puna and montane steppe faunas have about 413 species (16 % of South American birds). All high Andean avifaunas combined have a total of about 888 species (34 % of South American birds).

The number of species studied by the author and others corresponds so far to 74 % of the páramo-puna fauna (106 species), 24 % of the ceja fauna (123 species), and 34 % of the montane steppe fauna (113 species). Combining all three, the sample con-

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sists of 31 % (273 species) of the total high Andean fauna (888 species), or 10 % of the total South American fauna (2640 species). In the present paper I illustrate speciation phenomena qualitatively by examples. Nomenclature follows MEYER DE SCHAUENSEE (1966).

Geographical isolates within species

Inter-Andean disjunctions

(1) *Nothoprocta pentlandii* (Tinamidae). Montane steppes; southern Ecuador to northern Chile and south-central Argentina. Western Andean populations of southern Perú (*oustaleti*) are isolated from eastern Andean ones (*fulvescens*) by puna vegetation at higher altitudes, which are inhabited by *Nothoprocta ornata* (KOEPCKE, 1968).

(2) *Oxypogon guerinii* (Trochilidae). Páramo; Venezuela, Colombia. There are disjunct, but weakly differentiated populations; *cyanolaemus* (Santa Marta) is separated by the César Depression from *guerinii* (eastern Colombian Andes). The latter is isolated from *lindenii* (Mérida Andes) by the Táchira Depression and from *stuebelii* (Colombian Central Andes) by the Magdalena Valley (TODD & CARRIKER, 1922).

(3) *Myiotheretes rumigatus* (Tyrannidae). Ceja; Venezuela and Colombia to central Perú. There are three peripheral isolates in Perijá (weak differentiation: *olivacea*), Mérida Andes (differentiated: *lugubris*), and northwestern Perú (slight differentiation: *cajamarcae*). The remainder of the distribution suggests two large population continua, both assigned to the subspecies *fumigatus;* one is in Colombia-Ecuador, and is isolated from the other in eastern Perú. Barriers invoked to account for isolation include the Táchira Depression and the Northern Peruvian Low (VUILLEUMIER, 1971).

(4) *Oreomanes fraseri* (Coerebidae). *Polylepis* woodlands within páramo, puna; southern Colombia to western Bolivia. *O. fraseri* has a patchy distribution (about 15 more or less isolated populations) that is partly correlated with the distribution of *Polylepsis* habitat, and partly with barriers (Northern Peruvian Low, Apurimac Valley, etc.), but differentiation is weak (VUILLEUMIER, MS).

Extra-Andean disjunctions

(1) *Nothoprocta pentlandii.* In western Perú, deserts isolate Andean populations *(oustaleti)* from two differentiated coastal ones (*niethammeri* and unnamed). KOEPCKE (1968) suggested the two lowland isolates represented two independent colonizations from the Andes.

(2) *Agriornis microptera* (Tyrannidae). Puna; southern Perú, northern Chile, western Bolivia, northwestern Argentina (altiplano), and Patagonian tableland. The weakly differentiated Andean *(andecola)* and Patagonian *(microptera)* populations are separated by about 1000 km of montane terrain (VUILLEUMIER, 1971).

Geographical isolates between semi- or allospecies

Inter-Andean disjunctions

(1) *Oreotrochilus* (Trochilidae). Taxa *chimborazo* (Ecuadorian páramos) and *stolzmanni* (northern Peruvian puna and montane steppe) separated by the Northern Peru-

vian Low (Vuilleumier, 1967), are a borderline case, having been considered species by Berlioz & Jouanin (1942), but subspecies by Zimmer (1951).

(2) *Schizoeaca* (Furnariidae). Taxa *perijana, coryi, fuliginosa, vilacabambae, griseomurina, ayacuchensis, plengei, palpebralis, helleri,* and *harterti* (páramo and upper ceja from Perijá and Mérida to western Bolivia), form a chain of differentiated populations, each occupying a relatively restricted range. Some authors merged all taxa into a single species (e.g. Vaurie, 1971), whereas others recognized several species (e.g. Phelps, 1977). *Schizoeaca* possesses both borderline cases (e.g. within *fuliginosa* group) and allospecies (e.g. *coryi, harterti*). Barriers between isolates include the Táchira Depression (Vuilleumier & Ewert, 1978), the Northern Peruvian Low, and the canyon of the Huallaga, but other gaps are not so easily defined as barriers (O'Neill & Parker, 1976).

(3) *Asthenes* (Furnariidae). Taxa *pudibunda* (western slope, Peruvian Andes), *ottonis* (inter-Andean region, central-southern Perú), and *heterura* (eastern slope, Bolivian Andes) appear entirely allopatric in montane steppe, and separated from one another by high altitude puna occupied by unrelated *Asthenes* species. Treatment of these allopatric taxa (semispecies or allospecies) has varied from two (Meyer de Schauensee, 1966) to three species (Vaurie, 1971).

Extra-Andean disjunctions

(1) *Tinamotis* (Tinamidae). Taxa *pentlandii* (puna; altiplano of Perú, Bolivia, northern Chile, and northwestern Argentina) and *ingoufi* (Patagonia tableland) are two allospecies separated geographically by about 1000 km of montane terrain (Vuilleumier, 1967).

(2) *Asthenes.* Taxa *cactorum* (cactus-desert of coast and lower Andean slopes, western Perú) and *modesta* (puna; Perú to Bolivia) are two close relatives (considered species by Koepcke, 1965; subspecies by Vaurie, 1971) geographically isolated by montane steppes at intermediate altitudes, where the unrelated *A. pudibunda* lives (Koepcke, 1965).

Secondary contacts

Parapatry

(1) *Muscisaxicola* (Tyrannidae). In the *Muscisaxicola alpina* super-species (puna) *M. alpina* (*grisea* phenotype) contacts *M. cinerea* along the eastern Bolivian Andes. After field study I concluded (Vuilleumier, 1971) that the two semispecies occur in climatically different parts of the Andes, come in contact in several localities, but that geographical overlap between them is very slight.

(2) *Diglossa* (Coerebidae). Two sharply differentiated taxa of the *D. carbonaria* superspecies (upper ceja) meet in northern Perú: *D. humeralis aterrima* and *D. brunneiventris* (Vuilleumier, 1969 a). Personal field work in Cajamarca in 1975 suggested that these taxa are not separated by a barrier and are not hybridizing.

Hybridization

(1) *Colaptes* (Picidae). In the puna of north central Perú two well differentiated forms of *Colaptes rupicola (cinereicapillus* and *puna)* hybridize in Cerro de Pasco

(SHORT, 1972). Another area of hybridization seems to exist between *puna* and *rupicola* near Lake Titicaca. Both areas constitute what Short called filter barriers (partial ecological barriers).

(2) *Myiotheretes striaticollis.* Montane steppe; Venezuela and Colombia to northwestern Argentina. A "change from relatively large and dark birds to small and pale ones (with fewer and narrower throat streaks) seems to occur rather abruptly in southern Perú, and might be considered either as a step in a cline of north to south geographical variation, or as an instance of secondary hybridization" (VUILLEUMIER, 1971).

(3) *Diglossa.* Hybridization between *brunneiventris* and *carbonaria* (ceja) in La Paz, Bolivia, was reported (VUILLEUMIER, 1969 a). Later field and museum study suggested that the narrow hybrid zone does not coincide with a presently well-defined ecological barrier, such as a dry valley across the ceja. Differentiation might have occurred across the Rio La Paz, followed by colonization before reproductive isolation was completed (VUILLEUMIER, MS).

Marginal overlaps

(1) *Nothoprocta. N. curvirostris* (páramos and montane steppes; Ecuador, northern Perú) overlaps with its closest relative *N. pentlandii* in northwestern Perú, west of the upper Marañon Valley. Elsewhere, *curvirostris* occurs alone along the eastern Andes south to Huánuco, and *pentlandii* alone in Cuzco (VUILLEUMIER, 1967).

(2) *Oreotrochilus.* Overlap between *O. melanogaster* and *O. stolzmanni* involves only the southern portion of the range of *stolzmanni* and the northern of *melanogaster* (VUILLEUMIER, 1967). SHORT & MORONY (1969) described interspecific aggression and some habitat co-occupation between the two species in an area of sympatry in Cerro de Pasco.

(3) *Cistothorus* (Troglodytidae). The very extensive range of *C. platensis* (upper ceja, páramo, montane steppes) in the Andes includes two areas of overlap, in Venezuela with *C. meridae,* and in the eastern Colombian Andes with *C. apolinari.* In Venezuela, one finds altitudinal replacement rather than habitat overlap (VUILLEUMIER & EWERT, 1978). (Do the overlaps in *Cistothorus* represent double invasions?)

Broad range overlaps

(1) *Geositta* (Furnariidae). The closely related species *G. cunicularia* and *G. punensis* are broadly sympatric in the puna: the distribution of *punensis* (altiplano) is almost entirely enclosed in that of *cunicularia* (VUILLEUMIER, 1967). My field work in Bolivia in 1967 revealed that both species occupy the same habitat locally.

(2) *Agriornis.* Two closely related páramo-puna species, *A. montana* and *A. albicauda,* are sympatric from Ecuador to northern Chile and northwestern Argentina, where they seem to share habitats locally (VUILLEUMIER, 1971).

Discussion

Range discontinuities occur in many Non-Passerines, Non-Oscines, and Oscines living in páramo, puna, ceja, and montane steppes throughout the Andes. Differentiation

associated with inter- or extra-Andean disjunctions ranges from weak (subspecies) to strong (semispecies) and very strong (allospecies).

Only some range discontinuities, however, can be correlated with precisely defined eco-geographical barriers (VUILLEUMIER, 1977). In a few cases studied personally in the field, observed and mapped range disjunctions coincide with the presumed barriers (example: *Schizoeaca coryi* and *S. fuliginosa* in Venezuela; Táchira Depression). But in many other cases of differentiation in isolation, the latter is only approximately centered on an eco-geographical barrier (example: differentiation and disjunction of *Oxypogon guerinii lindenii* (Mérida) from *O. g. guerinii* (Cocuy) corresponds only in part with the Táchira Depression).

Still other discontinuities and some contact zones (with or without hybridization) occur in regions where no barrier seems to exist today (VUILLEUMIER, 1969 b), for example the extra-Andean disjunction in *Agriornis microptera,* or the hybridization between *Diglossa brunneiventris* and *carbonaria.* These areas seem to be located more often in the central than the northern Andes, and south of the central Andes.

Study of marginal range overlaps shows that some closely related species pairs may have only minor habitat differences in sympatry (example: *Oreotrochilus melanogaster* and *stolzmanni* in Perú). Study of broad range overlaps similarly suggests that in some instances at least, some degree of habitat co-occupation is achieved in sympatric species pairs presumed to have had a common ancestor (example: *Agriornis montana* and *albicauda*).

In many cases interspecific competition may influence latitudinal or altitudinal disjunction patterns (examples: *Nothoprocta pentlandii/ornata; Cistothorus meridae/platensis*).

Conclusions

Preliminary answers to the two questions asked in the Introduction can now be given.

(1) The data summarized in this paper suggest that speciation is presently favored throughout the high Andes wherever any kind of habitat discontinuity breaks up the range of species, centrally or peripherally. Such gaps are altitudinal or latitudinal. Some barriers are evident whereas others remain obscure.

(2) The data do not suggest directly how speciation occurred in the past. If barriers like those of today operated in the past, then were they in the same places, or elsewhere? Probably both, if present geographic barriers (deep valleys) have remained where they are, and if parapatry, stepped clines and hybrid zones are correctly interpreted to be located where barriers once existed. But intergradation and hybridization may be hard to interpret in terms of barriers (ENDLER, 1977).

Speciation patterns can nevertheless be correlated with Pleistocene events (CHAPMAN, 1940; VUILLEUMIER, 1969 b; HAFFER, 1970; PAYNTER, 1972; FITZPATRICK, 1973). Geological and palynological work shows the geographical extent and timing vegetational fluctuations during the Plio-Pleistocene (VAN DER HAMMEN, 1974; SALGADO-LABOURIAU et al., 1977; SCHUBERT, 1978; and others). Profound changes in climate and vegetation occurred over rather long time spans (glacial-interglacial cycles), minor ones over

shorter time spans. All these changes reveal the great three dimensional complexity of landscape evolution at any Andean locality.

One wonders, then, how realistic some correlations are, no matter how suggestive they may be. Extrapolations from present patterns of range disjunctions and the supposed effects of barriers, to the past, remain exercises in diagrammatic (Haffer, 1970; Van der Hammen, 1974) or verbal (Vuilleumier, 1969 b) model making. We can only suggest the relative probability of isolation today, so how can we do anything but guess where, when, and how isolation formerly occurred? Indeed, little is known about how disjunct populations differentiate or speciate. Thus, ornithologists are urged to launch detailed studies to document specific cases of isolation, or to survey unanalyzed genera.

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A Comparison of Suboscine and Oscine Radiation

Claes Chr. Olrog

Introduction

The mixed suboscine and oscine passerine avifauna of South America is rather complex, but it is not the aim of this paper to try to explain this matter, only to give a simple example comparing the ecological radiation of two suboscine insectivorous genera with two oscine granivorous genera, which live and overlap in the arid temperate and alpin brushlands in western and austral South America. Such scrub and open country habitats are usually rather well packed with species in the Andean and Patagonian areas chiefly furnarine and tyranine genera like *Geositta, Cinclodes, Upucerthia, Thripophaga* and *Muscisaxicola,* emberizine finches like *Phrygilus* and *Sicalis* and cardueline siskius. Insectivorous oscines are scarce, represented only by swallows and pipits and in some degree by omnivorous mockingbirds and thrushes. On the other hand there is a complete lack of granivorous suboscines, so there is practically no competition between the two groups, except possibly for nesting sites. Generally the furnarids, tyrant-flycatchers and finches are adapted in a rather convergent manner to distinct habitats from sea level towards 4000 meters altitude in the mountains, or from humid forests and marshes to arid scrub and steppes, being the predominant passerine families in South America. Although the number of species generally is high, often 10 or more per genus, most forms are of restricted distribution, two or three species of each genus have a wide range covering a great number of habitats and are currently divided into various subspecies with possible development towards full species. Such widely distributed species are here called predominant being the potential gene-bearers for future speciation.

Species involved

Selected at random for this study are the suboscine furnarine genera *Geositta* and *Upucerthia*, and the oscine emberizine genera *Phrygilus* and *Sicalis*; also included are some divergent but closely related monotypic genera like *Eremobius* and *Chilia* with *Upucerthia, Melanodera, Diuca* and *Idiopsar* with *Phrygilus* (Fig. 1). The number of species is about the same for each genus, the taxonomic differences being mainly due to body size and bill shape. The body size ranges from large to tiny, generally presenting three distinct sizes, except in *Upucerthia,* with only two. Three types of beaks can be noted in each genus indicating a certain tendency towards a parallel adaptation.

Bill shape and habitat selection

The four genera inhabit rather uniform biotas in arid brush-and grasslands with rocky, stony or sandy ground, being principally of terrestrial habits. We have no knowledge of the exact food selection of these birds, but the beaks are so differently shaped that it is reasonable to suppose that they do not really compete with each other, where they some times occur together; however, there is only a slight overlapping of

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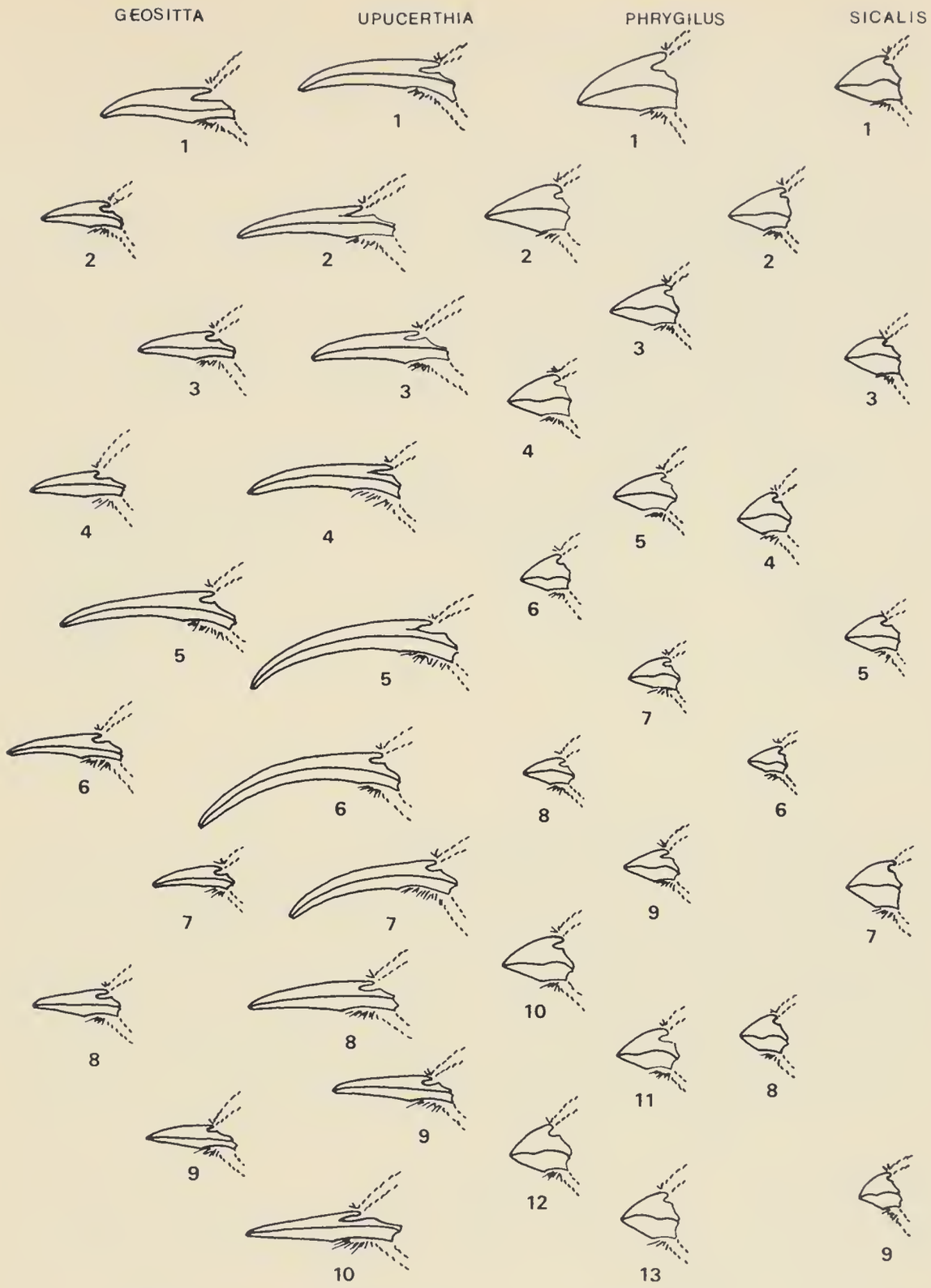

GEOSITTA
1. CRASSIROSTRIS
2. PERUVIANA
3. RUFIPENNIS
4. PUNENSIS
5. TENUIROSTRIS
6. CUNICULARIA
7. MARITIMA
8. ANTARCTICA
9. SAXIOLINA

UPUCERTHIA
1. SERRANA
2. CERTHIOIDES
3. HARTERTI
4. ANDAECOLA
5. DUMETARIA
6. VALIDIROSTRIS
7. JELSKII
8. RUFICAUDA
9. EREMOBIUS
10. CHILIA

PHRYGILUS ET.
1. IDIOPSAR
2. ATRICEPS
3. GAYI
4. PATAGONICUS
5. DORSALIS
6. MELANODERA
7. CARBONARIUS
8. PLEBEJUS
9. UNICOLOR
10. FRUTICETI
11. ALAUDINUS
12. DIUCA
13. XANTHOGRAMMA

SICALIS
1. LUTEA
2. AUREOVENTRIS
3. OLIVASCENS
4. LEBRUNI
5. UROPYGIALIS
6. CITRINA
7. LUTEOCEPHALA
8. FLAVEOLA
9. LUTEOLA

FIGURE 1

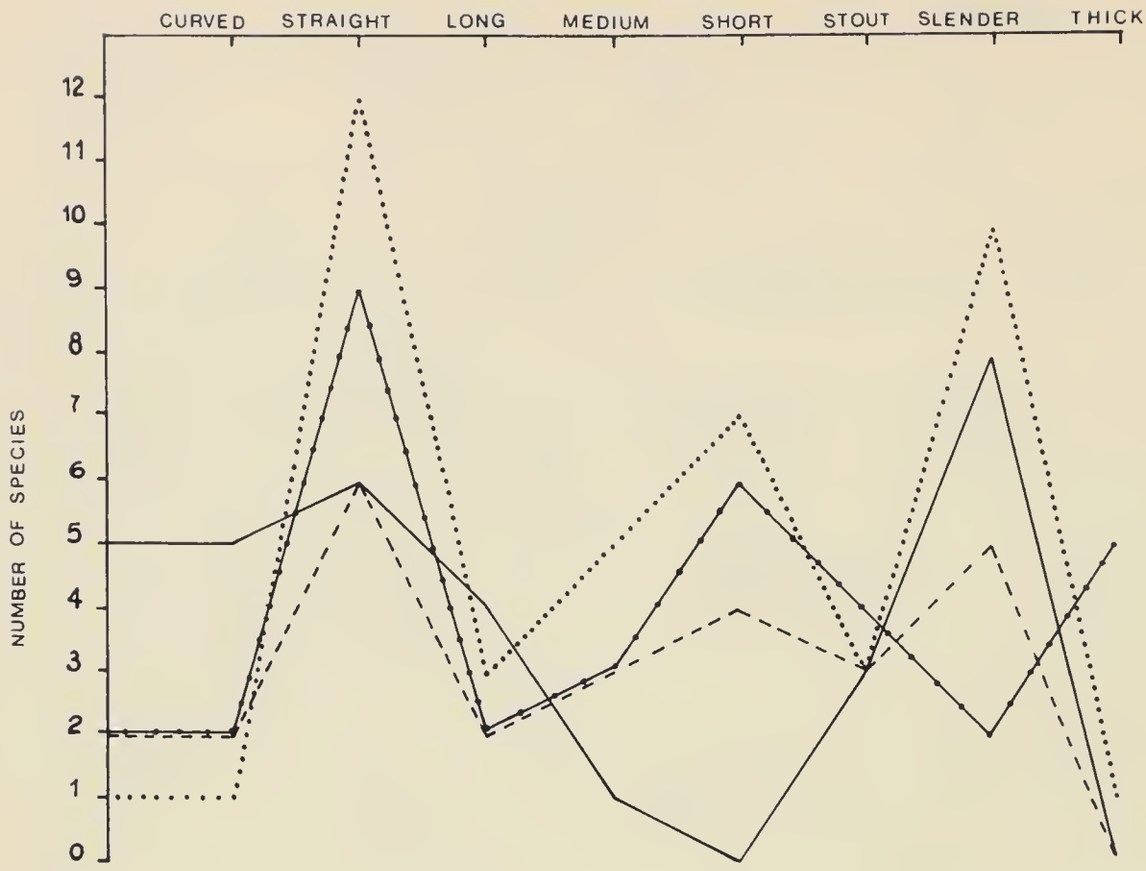

FIGURE 2. BILL SHAPES.

species with similar bills. The diversity of beaks is somewhat convergent, the most current on being straight and slender in the furnarids, slender and only slightly arched in the finches, while very few are stout or muched arched. Bill shape versus habitat indicates that the straight, medium and slender beaks are the most developed and the most common both latitudinally and altitudinally for the species of restricted range (Fig. 2). The general habitat selection shows a slight distinct pattern and that *Upucerthia* and *Phrygilus* and *Upucerthia* (Fig. 3) chiefly live in arid and stony brushlands, which the divergent related species also do, while sandy scrubby plains are the most current habitats for *Geositta* and *Sicalis;* only three finches are found in moist pastures and scrub.

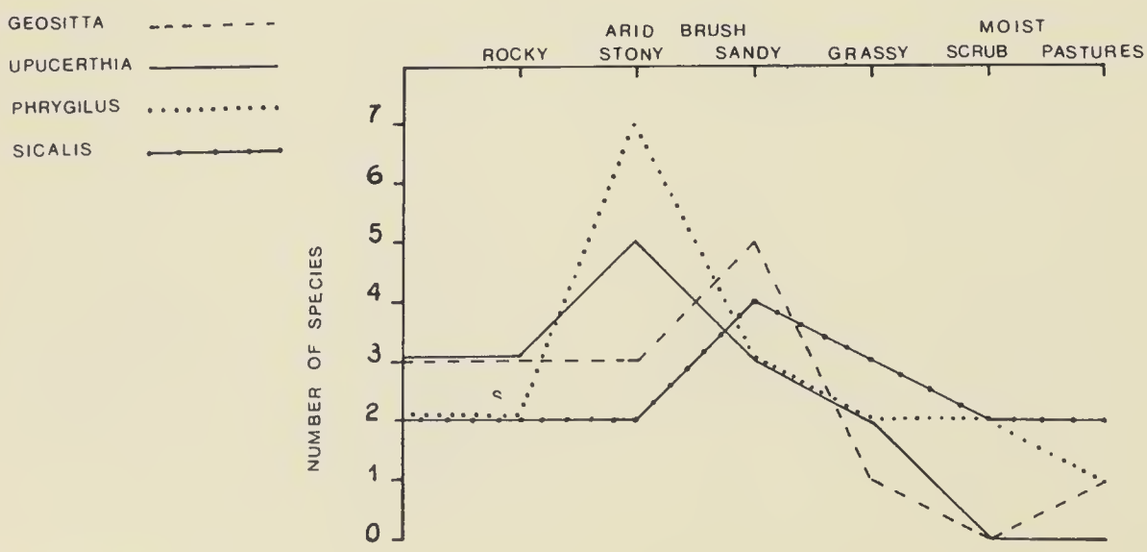

FIGURE 3. Habitats.

Predominant species

These forms do not follow the pattern of the small-ranged species, but show a remarkable difference in bill shape (Fig. 4). *Geositta* has one short and thick *(rufipennis)*, one medium long and slender *(cunicularia)*, *Upucerthia* one long and much curved *(dumetaria)*, another long and straight *(ruficauda)*. The three predominant *Phrygilus* show one long and slender *(gayi)*, one long and arched *(fruticeti)*, one small and thin *(unicolor)*, while in *Sicalis* there is one slender *(olivascens)*, two short and arched *(flaveola* and *luteola)*. The latitude range of the predominant furnarids is much narrower than in the finches, except *Sicalis olivascens*, while the elevational range is quite equal from sea level towards 3500 meters in the mountains, save the two other *Sicalis*.

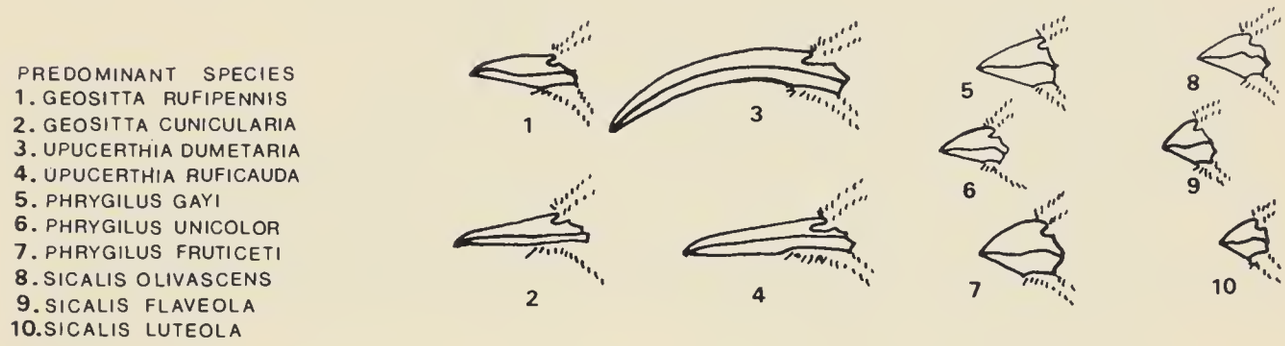

FIGURE 4. Predominant species.

Speciation centres

In order to obtain an idea where the centre or centres of speciation may be situated, the latitude range (Fig. 5, above) indicates that the principal area ought to have been between 15° and 20° South Latitude for the four genera involved, with another zone between 35° and 40° South Latitude. Regarding the narrow-ranged species today 15°, 40° and 50° South Latitude show the highest peaks. The elevational range (Fig. 5, below) is somewhat surprising, showing that the occurrence is more or less alike from sea level towards 3500 meters in the mountains, but with very few species inhabiting biotopes at 4000 and 4500 meters altitude. Climatic and life conditions are, however, much the same from 3500 meters altitude in Peru and Bolivia successively down towards sea level in Patagonia and Tierra del Fuego, but not with regard to the coastal strips of Peru and northern Chile, where the conditions are tropical. This might indicate that the general adaptation took place in the lowlands and valleys and that the high mountains have been colonized later or after the last glaciation. In this case one would presume that the granivorous finches, newcomers in South America, were first able to occupy their respective niches, followed later by the insectivorous furnarids. Still unknown, however, is which kind of granivorous passerines was replaced by the finches. Concerning the predominant species, they occupy today mainly the lower mountains, valleys and plains south of the Capricorne, with the majority of subspecific populations between 30° and 45° South Latitude possibly a recent centre of speciation exists in central western Argentina, where during the last years a fair number of new forms with the characteristics of semispecies or megasubspecies has been discovered in a well isolated area.

FIGURE 5. Above: latitudinal range; below: elevational range (heights in meters).

Conclusions

It seems rather clear that there has been a parallel adaptive radiation in two unrelated suboscine and oscine groups. The latitudinal and altitudinal ranges indicate that the same area is the main centre, harbouring a remarkable concentration of species. Such an area might have been the speciation centre as well. The fact that two of the predominant *Sicalis* species today are lowland forms should not be a significant objection since most species are more or less isolated in high mountains.

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Speciation in South American Woodpeckers

Lester L. Short

I recently completed a monograph of the world's 198 woodpeckers (Short, in press), and previously have treated speciation in African woodpeckers (Short, 1970, 1979). With the foundation provided by these works, it particularly is fitting that the patterns of speciation in the Picidae of South America, where the family is most numerous, be subjected to analysis.

The species of South American woodpeckers are according to Short (in press, see table there). The total number of species for the continent is 76, representing nine genera. This compares with 26 species in six genera for sub-Saharan Africa, and 50 species in 15 genera for tropical Asia. (The ratio of species to genera is interesting, but cannot be treated here; suffice to say that, despite these data, Africa is rather comparable in this ratio to South America, whereas Asia distinctly has more genera with fewer species.)

A major premise that I fully realize is not universal is that on the average the amount of genetic divergence is approximately directly correlated with the time two populations have had to diverge since sharing a common gene pool. That is, the longer the time for divergence, the greater the accumulation of genetic differences. This view is in accord with accepted evolutionary processes, and indeed it forms the foundation for most current taxonomic research. Of course there are exceptions, very rapid versus very slow divergence and speciation, or more commonly perhaps, rapid shifts that involve one or several but not all character complexes in a taxon. There also is the problem of equating observed phenotypic divergence with actual genetic divergence. However, by and large, and on the average there should be a rough correlation between divergence and time, such that even realizing that 100 percent success is unlikely, one can categorize divergence at levels of subspecies groups, allospecies (Amadon, 1966) of superspecies, closely related congeneric species, species groups, distantly related congeners, and genera in the framework of an increasing time span.

I analyze patterns of speciation in South American woodpeckers in four categories that reflect an increasing span of time required for divergence, namely: 1) major intraspecific derivatives, presumably recent in origin; 2) derivatives at or near the level of allospecies of superspecies, that is, entities, that have but recently speciated, assumed to be older generally than (1); 3) derivatives within species groups, assumed to be still older; and 4) derivatives more distinctly related, hence believed to be older yet.

The major intraspecific derivatives include well-marked subspecies, or "megasubspecies" (Amadon & Short, 1976). Of the 76 species, 19 are at this level and these 19 show 43 major subspecies of megasubspecies, many so distinct that they once were treated as species apart from those in which they now are merged. All of the differentiates are vieved as having originated allopatrically. Their current distribution suggests barriers that have isolated them geographically in the past.

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The 43 major subspecies or megasubspecies of the 19 species are engaged in 24 discrete situations, some of which show two fronts, hence there are 30 potential barriers to be explained. More than one separation have occured in *Picumnus cirratus,* with six major isolates or former isolates, and in *Piculus rubiginosus,* with three. Barriers affecting populations at this level number six that involve more than one species. Separation in Panama or adjacent northern Colombia allowed the evolution of distinctive forms north of this barrier, in Central America of *Piculus leucolaemus simplex,* and south of the barrier, in South America, of *Melanerpes formicivorus flavigula* and *Melanerpes chrysauchen pulcher.* Other major barriers acted: 1) between Guianan and northeast Amazonian and western Amazonian populations (to the east, the *elegans* group of *Celeus elegans* and the *rubrifrons* morph of *Melanerpes cruentatus* apparently evolved, isolated probably by a northsouth savanna intrusion); 2) in the east between Amazonian forests and the woodlands of northeastern Brazil (*Celeus elegans* and *Picumnus cirratus* involved here); 3) along the eastern slope of the Andes between Bolivia and Peru, affecting *Picumnus cirratus* and *Piculus rivolii;* 4) roughly between subtropical forest and savanna and the pampas, affecting *Colaptes melanochloro* and *C. campestris* (SHORT, 1972); and 5) between interior woodlands and the southeastern Brazilian forest, affecting *Picumnus cirratus* and *Dryocopus lineatus.* Less significant barriers affecting but one species number 17. All of these effects are judged to have occurred recently, i. e., isolation, differentiation and in many cases, renewed contact and interbreeding.

Older separations are reflected by contacts between populations that recently have achieved reproductive isolation. Most of these involve superspecies containing one or more allospecies. There are 24 interspecific interactions, some on several fronts and involving 36 species, two of which are Middle American (*Celeus castaneus* and *Campephilus guatemalensis*). Separation of the parts of the ancestral populations to allow speciation must have occurred in the late Pleistocene, perhaps during and just following the time of the Wisconsin glaciation.

Major barriers effecting these separations occured: 1) between Panama and adjacent Colombia, and interior or eastern Colombia (*Melanerpes pucherani-chrysauchen, Celeus castaneus-elegans,* and *Campephilus guatemalensis-melanoleucos* were involved); 2) between eastern Amazonian Brazil and woodlands of northeastern Brazil (*Melanerpes cruentatus-flavifrons, Colaptes punctigula-melanochloros,* and *Celeus elegans-flavescens* were involved); and 3) between the chaco and southeastern Brazilian forest (see SHORT, 1975; involved were *Piculus chrysochloros-aurulentus, Celeus lugubris-flavescens,* and *Dryocopus schulzi-lineatus).* Other barriers affected two species each, including a separation between Andean eastern and western Colombia (*Picumnus olivaceus-granadensis, Campephilus haematogaster-pollens),* another between the central and eastern Amazon *(Veniliornis affinis-cassini, Celeus grammicus-undatus),* a third between the Andean slopers of Bolivia-Argentina and the chaco *(Picoides lignarius-mixtus, Veniliornis frontalis-passerinus),* a fourth between the caatinga dry woods and southeastern Brazilian forest or woodlands (*Picumnus pygmaeus-albosquamatus, Veniliornis affinis-maculifrons),* and last, between forested southeastern Brazil and interior woodlands (*Picumnus cirratus-albosquamatus, Piculus aurulentus-chrysochloros).* There are seven or eight other minor barriers each affecting but two species.

More divergent, hence apt to be more ancient derivatives are forms of 28 species involved in 14 situations. There are no barriers indicated as affecting three or more

pairs of species. The Middle American-South American barrier probably separated ancestors of the superspecies *Melanerpes carolinus* and *Piculus rubiginosus* from southern Middle America northward and, respectively ancestors of *M. rubricapillus* and *P. rivolii* in northern South America. Subsequent to their speciation, *P. rubiginosus* extended into Andean and northern South America, and *M. rubricapillus* invaded Middle America, such that each is sympatric with its near relative. Isolation followed by speciation east of the Andes and west of them in Colombia (also Middle America) seems likely for the lowland pairs *Piculus leucolaemus—P. flavigula,* and *Celeus loricatus* and the superspecies *C. undatus. Piculus leucolaemus* subsequently has invaded the western Amazonian lowlands and there is sympatric with *P. flavigula,* but *C. loricatus* remains allopatric with the two allospecies *Celeus undatus* and *C. grammicus* of the superspecies *C. undatus.* In the Andes of eastern Peru some barrier separated the ancestors of *Picumnus castelnau* and *Veniliornis dignus* to the north, and ancestors of *P. subtilis* and *V. nigriceps* to the south. Today *P. castelnau* and *P. subtilis* barely are sympatric in Peru, but *P. dignus* and *P. nigriceps* have expanded their ranges respectively southward and (especially) northward along the Andes to become broadly sympatric. Barriers affecting only a single pair of species isolated ancestors of eight other pairs of species.

I suggest seven situations that may reflect very old derivations, and the operation of barriers far back in the Pleistocene. The location of these putative barriers is more open to question than in the case of later derivations. There are five former barrier situations each affecting a pair of species, and one affecting two pairs. The two pairs in the latter case are *Melanerpes cactorum-Melanerpes [cruentatus]* and the ancestors of *Campephilus leucopogon-C. magellanicus* and *C. [melanoleucos]-C. robustus.* Their isolation may have occurred in the eastern fringes of the chaco or slightly to the east, perhaps through inundation of the Parana-Paraguay river region, isolating ancestral *M. cactorum* and the ancestor of *Campephilus leucopogon-C. magellanicus* to the west, and their corresponding relatives, respectively ancestral *M. [cruentatus]* and the ancestor of *C. [melanoleucos]* and *C. robustus,* in the east. The other separations involved: 1) the ancestor of *Melanerpes formicivorus* in Middle America from that of the superspecies *M. cruentatus* in South America (Panamanian barrier?); 2) the ancestors of *Picumnus minutissimus* complex north of the Amazon and of the *P. cirratus* complex to the south; 3) the ancestor of *Veniliornis dignus* and *V. nigriceps* in the Andean region from that of the superspecies *V. passerinus* somewhere to the east in Amazonia; 4) the ancestor of *Colaptes rupicola* and *C. pitius* in the Andes from that of *C. campestris* in open country somewhere to the east of the central and southern Andes: and 5) the ancestor of *Dryocopus galeatus* and that of the superspecies *D. pileatus* between southeastern Brazilian forest and Amazonian forests.

When one views the differential isolation of these taxa in relation to their systematic affinities, presumably correlated with their ages of origin, there appear certain recurrent patterns, and others that seem restricted to either younger or older situations. Repeated patterns include disjunction; 1) between Middle and South America, 2) between southeastern Brazil and the interior (both north and west of there), and 3) between the Andes Mountains (or some altitudinal level therein) and lowlands to the east. The first of these reflects both water gaps between South America and Middle America in Panama, and more recent vegetational, perhaps wet-dry cycles that for

example must have caused separation of moist forest forms by interposition of drier habitat (HAFFER 1969, 1970, 1974a, 1974b). Southeastern Brazilian moist forests are a strong center of endemism, as evidenced by the many species restricted to that region. Its forests largely seem to have been isolated from forests elsewhere (e. g., Amazonia) by grasslands (savannas) or woodlands (chaco, campo, caatinga) of the interior (see, e. g., the fragmented ranges of *Manacus manacus* and *Pteroglossus aracari* shown by HAFFER, 1974a). Interior woodlands of today continue to separate forest areas, and thus forest birds, although birds of the forest edge that can tolerate woodlands may extend through the woodlands in riparian situations.

Throughout the Pleistocene the rising Andes Mountains must have affected climates and the distribution of forests on their slopes and in the vast lowland area to the east (and narrow western coastal lowlands as well). The much dissected valleys of the Andes vary in habitat with elevation and location generally, and their connections and separations have permitted speciation of local endemics, resulting in highly local species that afford the greatest number of avian species remaining to be described, as well as creating barriers to the distribution of high-altitude and submontane species, permitting divergence of the isolates (see VUILLEUMIER, 1970). Interdigitation of dry woodlands at the base of Andes and in lower Andean valleys, between moist submontane and moist lowland forest has resulted in isolation and divergence of lowland and highland or Andean slope populations. However some of the situations involving replacement species in higher and lower forested Andean slopes undoubtedly resulted from essentially north-south separation, caused by valley barriers, and subsequent contact and replacement of the newly speciated forms through their interaction, such that they tend to occupy higher and lower forest in bands along the eastern face of the mountains. The ranges of species pairs such as *Veniliornis dignis* and *V. nigriceps,* and *Piculus rivolii* and *P. rubiginosus* indicate a past north-south distribution.

Some of the barriers that appear to have acted in more recent times, but show little or no evidence of efficacy in more ancient times include: 1) north-south barriers in eastern Brazil; 2) campochaco barriers; 3) non-forest barriers between eastern and western Amazonia; and 4) Andean north-south barriers.

In general, barriers that seem to have affected woodpecker speciation relate only very broadly to the refugia scheme advocated by HAFFER (1969, 1974a, 1974b) and others. It is difficult if not impossible to establish, for example, whether a western versus eastern Amazonian isolation involved Haffer's Napo or East Peruvian refugia in the west, or one or another of his two (or four, see HAFFER 1969) eastern Amazonian refuges. Partly this may reflect the rather broad ecological tolerance of woodpeckers for trees of diverse types; so long as picid competition between close relatives is avoided it seems that woodpeckers can occupy accessible forest areas. Some refugia are clearly indicated, such as that in southeastern Brazil (without indications of where within that region), and the Belem versus Guiana refugium in eastern Brazil.

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Some Aspects of Speciation in South American Flycatchers

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The family Tyrannidae, with about 330 breeding species in South America, is the most diverse bird family in the New World. Throughout the continent, tyrannids comprise the dominant passerine family in all habitats from sea level to snow line. The family's ubiquity and diversity make it an ideal group for the study of biogeographic patterns in South America. Because discussion of speciation requires drawing inferences from present-day distributions, I begin this paper by summarizing the overall diversity patterns in the Tyrannidae and in its component lineages. Two groups in particular demonstrate important biogeographic consequences of a rich history of recent speciation, and these are discussed in the second part of this paper.

Diversity patterns in South American Tyrannidae

Figure 1 shows the numbers of breeding tyrannid species over the continent. Overall, flycatcher diversity is remarkably uniform throughout northern and Andean South America, despite the existence of numerous small and localized distributions within the family. The largest numbers of sympatric tyrannids occur in the forests of Amazonia, the central Andes, and southeastern Brasil.

Figure 1. Species density isoclines of breeding Tyrannidae in South America.

When plotted separately, the diversity patterns of the seven major phylogenetic lineages differ markedly from the overall pattern of Fig. 1. The most important contrast between the lineages lies in their respective sensitivities to the major vegetation bound-

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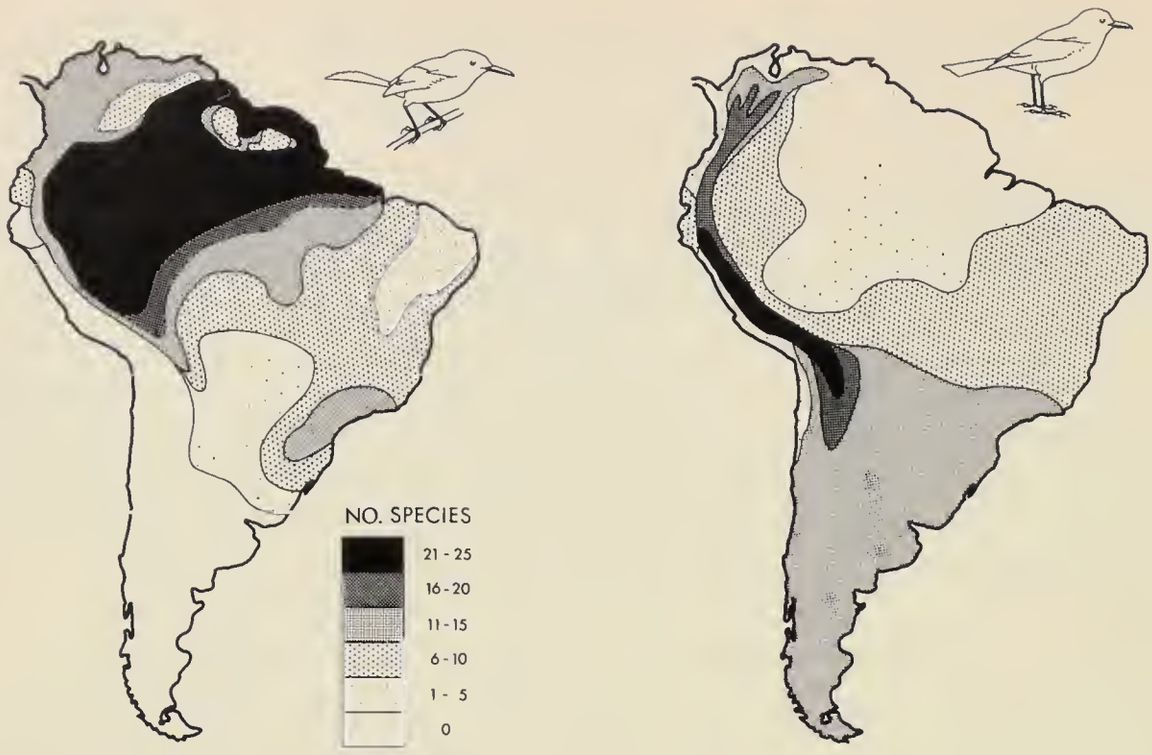

FIGURE 2. Species density isoclines for two phylogenetic lineages of ecologically specialized tyrannids. The Pygmy-tyrants (left) are largely restricted to forested habitats, and speciation has been most prolific within Amazonia. One fluvicoline lineage (right) is behaviorally restricted to open formations, leading to important speciation centers in the temperate Andes and in southern South America.

aries of the continent. Certain groups (e. g. Tyranninae and the frugivorous Elaeniinae, see TRAYLOR, 1977; FITZPATRICK, 1978) are distributed uniformly across lowland South America, showing no change in species density between forest and non-forest habitats. In contrast, two groups react strongly to the boundaries of the forested zones (Fig. 2). one is largely restricted to lowland, humid forest regions, while the other is nearly absent from these areas but is widespread within the open formations of the temperate Andes and southern South America.

These different diversity patterns reflect ecological differences between the groups. Those that show little sensitivity to major habitat boundaries are, for the most part, generalists in both foraging technique (FITZPATRICK, 1978) and habitat preference (in prep.). They show preferences for scrub and forest-edge micro-habitas, and they treat the forest canopy as if it were an elevated scrub. Because these species occupy the upper strata of both scrub and forest, their distributions tend to be large, and they show little coincidence with forest boundaries. Speciation patterns within generalist lineages are often obscured by broadly overlapping ranges that span much of the continent. These groups are not discussed further in this paper.

The small-bodied, broad-billed elaeniine species, formerly comprising the bulk of the subfamily Euscarthminae (HELLMAYR, 1927; hereafter referred to as Pygmy-tyrants), represent a specialized lineage in both behavior and morphology (FITZPATRICK, 1978). They are restricted to dense vegetation. Presumably because of their uniformity in size and foraging tactics, few of these species successfully coexist in the structurally simple habitats of the non-forested tropics. However, in the varied micro-habitats of

forested regions, sharp habitat partitioning (Fitzpatrick, in prep.) permits many forms to live sympatrically (e. g. Terborgh & Weske, 1969), as shown in Fig. 2. This restriction of most forms to forested habitats means that speciation has depended upon the history of the Amazonian habitats, probably coinciding with the cyclic contractions and expansions of the tropical forests (Haffer, 1974; Fitzpatrick, 1976). As discussed below, speciation and extinction patterns in this group demonstrate an important interplay between differentiation and competition within Amazonian birds.

About 65 species comprise a second assemblage of related forms that also show habitat restriction (genera *Sayornis* through *Muscipipra* in Traylor, 1977). This lineage, which includes the Ground Tyrants treated by Smith & Vuilleumier (1971), has behaviorally and morphologically specialized in ground-related foraging techniques (Fitzpatrick, 1978). These techniques require open micro-habitats (pampas, campo, cerroda, puna, and rocky slopes). This habitat restriction is reflected in the overall distribution of the group (Fig. 2). The few species that do occur in the forested regions of South America are restricted to marshes, beaches, and river edges that structurally resemble non-forested habitats. Thus, because of ecological restrictions, speciation in this fluvicoline lineage has primarily occurred in the temperate Andes and the semi-arid open formations of southern South America. Smith & Vuilleumier (1971) present an excellent treatment of Ground Tyrant speciation in the high Andes. Below, I discuss one common pattern of lowland speciation that strongly implicates the Paraguayan chaco as a region of secondary contact between recently speciated forms.

Speciation-extinction cycle among Amazonian Pygmy-tyrants

Within the Pygmy-tyrant lineage, repeated speciation in Amazonia has resulted in an intense build-up of species sharing extremely similar behavioral specialties. The ecology of these species is such that sharp micro-habitat segregation is possible. It appears to have been realized through competitive interactions between the species (some evidence in Slud, 1964; Haverschmidt, 1968; Fitzpatrick in prep.). Many of the present distributions of species groups show patterns of parapatry that support Haffer's (1974) hypothesized Amazonian forest refuges, which appear to have given rise to a number of sibling species complexes (Fitzpatrick, 1976).

Among the Pygmy-tyrants, however, there exists another common distribution pattern that requires more than a simple refuge hypothesis for its explanation. Certain groups of closely related species show peculiarly small and/or ecologically unique distributions, in which related forms may be separated by large gaps within an apparently uniform forest habitat (Fig. 3). It is insufficient to propose that the current ranges simply reflect ancient refugia. Such cases imply that some external pressure has limited the expansion of the species' distributions. Indeed, many of the ranges are so localized (e. g. *Hemitriccus mirandae, Todirostrum calopterum)* or discontinuous (e. g. *Hemitriccus rufigulare)* as to suggest that they have actually contracted from formerly more extensive distributions. Other characteristics of these groups include, (1) restriction to low or middle elevations on forested mountains around the Amazonian perimeter (e.g. *Hemitriccus granadense, H. furcatus, H. mirandae* superspecies; *Poecilotriccus ruficeps; Todirostrum calopterum)* (2) extreme rarity *(Todirostrum senex, Poecilotriccus andrei, Hemitriccus josephinae, Lophotriccus eulophotes);* (3) restriction to small, isolated mountain

ridges, where island effects have reduced the numbers of sourrounding competitors (Terborgh & Weske, 1975; e.g. *Hemitriccus rufigulare, H.* sp. nov.) *Todirostrum russatum, Hemitriccus furcatus);* (4) morphological peculiarity, as compared with the remainder of the group (e.g. *Poecilotriccus capitale, P. andrei; Todirostrum calopterum; Hemitriccus furcatus).*

All the above characteristics support my earlier hypothesis (Fitzpatrick, 1976) that these assemblages are relict species groups, showing the final stages in an Amazonian speciation-extinction cycle. Continent-wide species diversity increases through the cyclic production of new species in forest refugia, and competitive pressures upon each species increase. As successful species disperse through a continuous Amazonian forest, competitively inferior forms are forced to occupy progressively smaller ranges. Surviving populations are fragmented. Morphological and ecological divergence from the primitive condition are favored, including shifts to subtropical elevations and/or peculiar habitats. In the final stages, a species may exist only in relatively competitor-free regions, such as isolated mountain ridges.

Figure 3. Selected Pygmy-tyrant distributions. *Hemitriccus* and *Poecilotriccus* contain relict species groups (upper and middle) showing the final stages of an Amazonian speciation-extinction cycle. The patchy distribution of *Hemitriccus zosterops* (lower) may show current speciation that has resulted from competitively induced fragmentation of a formerly widespread species.

Interspecific competition is a critical ingredient driving this series of events. For this reason, the Pygmy-tyrants form an assemblage well suited for the study of this process. Their diversity in Amazonia is coupled with behavioral and morphological stereotypy such that intense competition is inevitable as ranges expand. In this regard, one attribute of certain Pygmy-tyrant distributions warrants emphasis, because it suggests the existence of a speciation process that is as yet little recognized by biogeographers. If a species' distribution can be fragmented by the spread of competitively superior forms within Amazonia, the remnant populations themselves may begin differentiating. If such a population is able to survive over a long period, it has the potential to diverge

significantly from its sister populations, and might even be able to reinvade a formerly occupied area.

The best evidence that this process is occurring lies in species that show multiple, disjunct, and well differentiated populations within Amazonia. These cases are not common, but they do exist: Fig. 3 shows the remnant populations of *Hemitriccus zosterops,* each of which is recognized as a distinct race. Other examples may exist in *Todirostrum calopterum* and *Poecilotriccus capitale.*

This process of competitively induced speciation gives rise to species groups that cannot easily be distinguished from populations still restricted to former refugia. This observation suggests that alternative hypotheses to refugium fragmentation must be considered when studying present-day distributions of endemic species.

Speciation in the "Arid Diagonal"

Of 80 tyrannid species that occur in the southeastern Brasilian forests, 32 (40 %) are isolated populations in that region, with closely related forms occupying Amazonian or Andean forests. This is a common pattern: species or subspecies pairs of many kinds of forest birds are separated by a diagonal swath of dry, open habitats stretching from northeastern Brasil south to the Argentine pampas. VANZOLINI (1974) refers to this as the "diagonal of open formations".

The simplest explanation for the above pattern is that the two, currently separate forest zones have at some point been contiguous, thereby permitting faunal exchange between them. VANZOLINI (pers. comm.) believes this to have been the case on the basis of lizard distributions. Given the extent of the Pleistocene vegetational fluctuations now documented for the rest of lowland South America (HAFFER, 1974), this explanation seems reasonable. The incursion of a forest bridge through the arid diagonal may actually have occurred several times in conjunction with the cycle shifts in the Pleistocene climate of South America.

If the northern and southeastern forests were joined for any extended period, we would expect to find evidence for this in the bird species that have historically been restricted to open formations. Such evidence is indeed most conclusive within the fluvicoline tyrannids that, as shown in Fig. 2, are confined to open habitats. In a number of tyrannid species, one subspecies occupies northeastern Brasil while another is found in Brasil, Paraguay, and Argentina. Examples include *Xolmis irupero, Tyrannus savana, Empidonomus auranteoatrocristatus, Euscarthmus meloryphus,* and *Stigmatura budytoides.* Many additional open country forms show continuous distributions along the arid diagonal, where two intergrading races occupy the two ends of the diagonal. These cases suggest that a recent barrier across the diagonal has caused southern and northeastern populations to differentiate slightly but not completely.

The more ecologically interesting situation along these open habitats arises among full species pairs, several of which are illustrated in Fig. 4. These pairs also given evidence for differentiation on either side of an ecological barrier (presumably forest). However, secondary contact has occurred between many of the pairs, giving rise to an important zone of interaction in the northeastern border of the chaco. SHORT (1975) provides numerous examples that show this area to be rich with species pairs currently interacting along their distributional boundaries. SHORT (1975, p. 346) says, "grassland

is apt to have been the major isolating factor creating a barrier to the east of the chaco." As mentioned above, the evidence that forests once connected southeastern Brasil with Amazonia and the Andes strongly points to this as the probable habitat barrier isolating these species pairs, many of which are obligate inhabitants of grassy habitats.

Whatever the barrier consisted of, however, the ecological implications are unequivocal: among South American open country tyrannids, the northeastern chaco forms the single most important zone of secondary contact between close relatives on the continent.

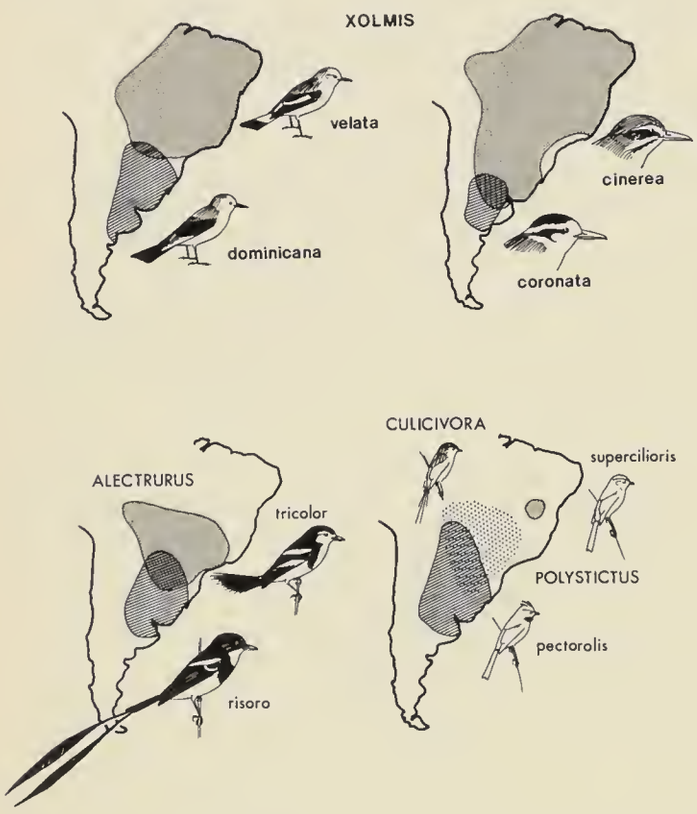

FIGURE 4. A common pattern of species pairs in the "diagonal of open formations" of southern South America. Secondary contact, usually near the Paraguayan chaco, is frequent between such pairs. Genera *Culicivora* (one species) and *Polystictus* (two species) are closely related. The former species, the result of an earlier speciation, now separates the two latter species and may actually be preventing their contact across the open formation diagonal.

The documentation of speciation patterns becomes especially important when this information provides a foundation for studying the dynamic relationships between species. Adequate study of how competitive relationships give rise to divergence, character displacement, and geographical or micro-habitat replacements depends on this information. Because open country tyrannids are common and easily studied, the situation described here presents an ideal arena for examining the ecology of secondary contact within a variety of species pairs.

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SYMPOSIUM ON
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The Status of Historical Biogeography

Ian Ball

Introduction

In his introduction to Hall & Moreau's splendid Atlas of Speciation of African Birds, Mayr (1970a) wrote that one of the most characteristic aspects of biological phenomena is that they always reflect past history and that the search for historical causes is the major preoccupation of the biogeographer and comparative evolutionist. Some philosophers of science have claimed that because the evolution of organisms is an historical process that relies on unique and unpredictable events it is not amenable to the formulation of testable theories. Interestingly enough many philosophers of history would not take this view for their own field of enquiry. More telling is the viewpoint of Polanyi (1964) that the practise of science in general is an art because there are rules that cannot always be made explicit or articulated in that they are not known or recognized by the scientists that follow them (see also Phillips, 1977). Nowhere in biology, I submit, is this more evident than in historical biogeography, a field that lacks an explicit theoretical and methodological framework (Illies, 1974; Cracraft, 1975). Within the compass of this brief essay I cannot hope to resolve this problem here, but I shall try to add illumination from historical, philosophical, and scientific perspectives with the aim of stimulating constructive debate in a field becoming increasingly controversial (Ball, 1975; McDowall, 1978).

Axioms and principles

In attempting to overcome the supposed short-comings alluded to above sets of principles for biogeography have been proposed by a number of authors including Cain (1944), Darlington (1957), Mackerras (1970), Løvtrup (1973) and Illies (1974). For the most part these principles as totalities are disappointing, principally for three reasons. They often are applicable to biogeography only in their generalities, there is usually a failure to distinguish between the axiomatic and the methodological, and they are frequently contradictory. Illies (1974), for example, gives six basic principles of causal zoogeography which fall into three groups of completely antithetical statements. Now, whereas these may draw attention to the variety of phenomena faced by a biogeographer they cannot be said to be the principles on which to formulate a science of biogeography.

Biogeography is concerned with the analysis (description and explanation) of the distribution patterns exhibited by living organisms. To commence a study of causal biogeography as historical biogeography only three basic statements, as axioms, are necessary:

a) Organic evolution has occurred and thus living organisms have a phylogenetic history.

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b) The surface of the earth has undergone change with time (i.e. configurations and sizes of the various land and water masses have not been stable).

c) Processes (a) and (b) have occurred concurrently since the time of origin of life.

From these basic beliefs, and with the assistance of auxiliary hypotheses in biology, further inferences can be made. Thus from (a) and current views of speciation (Mayr, 1970b) we infer that at the time of their origin all taxa had a restricted distributional range. From (a) and the empirical facts that extinction and cosmopolitanism occur we infer that the ranges of organisms have changed with time. And from axioms (b) and (c) and the above inferences we further infer that the patterns of biotic distributions have changed with time. These statements form the basis of all historical biogeography.

The data for analysis

Statements concerning patterns of biotic distribution may be made at the level of the character, species, higher taxon, or a total biota. It seems self-evident that whatever unit we choose should have reality in the sense that it represents something that exists in the objective world. Surprisingly, this principle is still frequently flouted by biogeographers.

Most biogeography rightly deals with the taxonomic units, the species and higher taxa. The species problem is a hoary one which I shall side-step by assuming the objective reality of the species, whether reproductively or morphologically delimited, as it is used by current biogeographers. Regarding the higher taxa it seems evident from the first axiom (a) that they, too, must have an objective existence. They exist as monophyletic groups as defined and recognized by the proponents of Phylogenetic Systematics (Hennig, 1966; Brundin, 1966). Whether or not such monophyletic groups should form the basis of a formal classification (Mayr, 1974) is not the question here at issue, but whatever classificatory system is followed the necessity remains that all comparative biology must deal in groups that exist, that represent the products of phylogenies. Any biogeographical theory that deals explicitly with non-monophyletic groups must be trivial or meaningless (Ball, 1975). Key (1976), for example, explicitly rejects the necessity for a prior phylogenetic analysis apparently without realizing the consequences of this rejection. In demanding a prior phylogenetic analysis I am seeking only that the units of analysis should have some objective reality. I am not requiring that the phylogenetic reconstruction be used to infer directions of dispersal, or centres of primitive or derived taxa.

I wish here to add a few words on the facts of scientific and historical enquiry. The empiricist and positivist positions of assigning prime importance to basic unadulterated facts are being swept away. It is now fashionable to accept the subjectivity of even the simplest facts in the sense that all facts are theory-laden, a point succinctly made by Medawar (1969): "unbiased observation is a myth". But it has not always been clearly understood that bias occurs not only in assessment but also in selection.

The facts of any historical enquiry are simply those that have been selected as worthy of consideration. As Carr (1964) put it, millions have crossed the Rubicon, but only one crossing, that of Julius Caesar, is considered a fact of history. There is little doubt that we select facts, consciously or unconsciously, in an analogous manner. Most commonly this can be seen in those taxonomists who restrict themselves to one particu-

lar character-suite in their organisms, usually for reasons of supposed conservatism in the character-suite, or of actual conservatism in the taxonomists themselves. It can also be seen in those biogeographers who select groups as worthy of study on the basis of "teleological deductions from the writing desk" concerning unstudied dispersal capacities (see Talling, 1951). The fact that the collection of basic data always takes place under the influence of some prevailing world-view or theoretical framework (paradigm) is the primary reason why it takes time for a new paradigm to achieve its maximum value, for new facts must be gathered and old facts re-assessed; until then the results inevitably will have imperfections. This seems not always to have been considered by critics of new paradigms in evolutionary biology, such as that of Phylogenetic Systematics (e.g. Blackwelder, 1977), and no doubt the fate of new world-views of biogeography will be the same.

Hypotheses

Here I consider an hypothesis to be an explanation in causal historical terms of an observed biotic distribution. As the word itself implies an hypothesis falls short of being an assertion; it articulates something not yet known to be true or false (Hanson, 1970). Before an hypothesis becomes the legitimate property of the scientific community it must pass through the three stages of erection, selection, and testing.

The erection of an hypothesis is outside the realm of logic; it is a creative act (Feyerabend, 1975). No one deliberately erects an hypothesis that is discordant with the facts to be explained, thus, since there are often many competing hypotheses for a given data-set it follows that concordance with the facts is not a measure of truth. This has not always been properly understood. If modern vertebrate distribution patterns are consistent with models of both stable and drifting continents (Darlington, 1965; Mayr, 1972) then the data base is insufficiently understood, or the biogeographical hypothesis is too general to be of significance. The derivation of an hypothesis may be aided by such rules as the progression rule, Matthew's rule, or the various rules for determining centres of origin and dispersal. But these rules in no way guarantee the validity of the hypothesis, which must be subject to independent test.

Hitherto many, if not most, hypotheses in historical biogeography have been formulated as narratives, as I have explained and criticised previously (Ball, 1975). Such narratives cannot be tested. They function like the "explanation sketches" of historians, pointing to the possibility and desirability of more detailed research (Gallie, 1968). From this the narrative perhaps may be made more restrictive and thus testable. A choice between competing narratives usually can be made only arbitrarily. And because the facts are influenced by the prevailing paradigm competition between hypotheses within the paradigm is weak. Strong competition occurs only when two theories from different paradigms clash (Feyerabend, 1970). This is partly exemplified by the debate between representatives of the three major schools of thought in historical biogeography (discussed in Cracraft, 1975), viz. Darlington (1957, 1970), Brundin (1966, 1972), and Croizat et. al. (1974). In this case resolution has been weak because the argument was concerned mostly with "a priorisms" rather than with the deductive consequences of rigourously formulated hypotheses.

Testability

A chosen hypothesis must pass several forms of test before it becomes incorporated into the fabric of science. Implicitly or explicitly it will be tested for internal consistency (rejection of self-contradiction or illogicallity), explanatory value (rejection of tautology), and for consistency with other hypotheses commonly accepted in the particular field of science. Ultimately it must be tested empirically.

In recent years some evolutionary biologists and biogeographers have attempted to reformulate their work within the framework provided by the philosophy of Karl Popper (Bock, 1973; Wiley, 1975; Ball, 1975). Their emphasis of Popper's theory has been on the so-called criterion of demarcation between science and non-science (or pseudoscience). The activities of scientists are normally concerned with the formulation of laws, the search for universal truths. The universal propositions that form the basis of all the Natural Sciences are of two types, the numerically universal and the strictly universal. Numerically universal statements are in principle both verifiable and falsifiable. Strictly universal statements are not in principle verifiable, they are only falsifiable. The asymmetry between proof and disproof is thus an unavoidable consequence of the logical structure of strictly universal statements. Testing implies attempts to falsify, and potential falsifiability forms a criterion of demarcation between science and non-science.

But as we have seen evolutionary biology is concerned with historical statements, with the elucidation of actual and unique events. Thus Kitts (1977) proposes that since the knowledge claims of systematic zoology are not expressed in strictly universal statements they are different from the knowledge claims of scientific theories. Kneale (1974) has previously made the same point, albeit in a different way.

I believe, however, that Kitts has not fully understood Popper's position. Popper himself (1961) has acknowledged that history is characterized by its interest in actual, singular, or specific events, but he goes on to say that this is perfectly compatible with his analysis of scientific method. Historical sciences take all kinds of universal laws for granted. The two tasks of historical enquiry, the disentanglement of causal threads, and the actual description of the way in which they are interwoven, are both necessary. Under the principles followed in this essay a biogeographical hypothesis would explain an historical event with the aid of auxiliary non-historical hypotheses relating to comparative morphology, and genetics, ecology, and so forth.

There is a further answer to Kitts. Whereas it may be true that the significance of falsifiability was revealed by consideration of strict universals this does not imply that they alone form the content of science. Popper claims only that a theory, to be scientific, should have the possibility of a clash with test statements, and clearly this can include some, but not necessarily all, singular historical statements (Popper, 1974). Furthermore, if it is true that the contingent barriers to the verification of the statements of systematic zoology are immense, even insurmountable (Kitts, 1977), then the only rational critical approach to their testing is to emphasize falsification.

Conclusions

The implications of what I have said are, I think, as follows. Historical biogeography, despite its emphasis on unique historical events, can be an empirical science by the

criteria proposed by Karl Popper. When hypotheses are founded on an adequate phylogenetic analysis then the explanatory models may be hypothetico-deductive and directly falsifiable statements may be readily derived from them either in terms of further phylogenetic investigation or further distributional information (Ball, 1975). Not all narrative explanations, however, will necessarily fulfill the criterion of demarcation. Their potential for conflict with observation-statements will depend upon their overall restrictiveness and the extent to which they are based on auxiliary hypotheses that are themselves open to test (Popper, 1974). If the narratives are too general then they will agree with every possible situation and no test will be forthcoming. Thus, to use an example quoted earlier, if the vertebrate distribution patterns as studied and explained by Darlington (1957) are compatible with both the dispersalist and vicariance paradigms (Darlington, 1965) then no conflict is possible. The explanation is at too general a level and can be neither falsified nor verified. Further analysis is required to achieve a truly scientific explanation.

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Dynamic Equilibrium Island Biogeography: The Second Stage

Daniel Simberloff

Many ornithologists enthusiastically endorse the dynamic equilibrium theory of island biogeography (MacArthur & Wilson, 1967), that island biotas are an equilibrium between immigration of new species and local extinction of extant ones (Simberloff, 1974); the concept has even been extended to the avifaunas of habitat islands like páramos (Vuilleumier, 1970). The theory neatly explains the well-known species-area relationship, that large islands have more species than small ones, as caused by lowered extinction rates because all populations are larger on larger islands. It explains the increasing avifaunal impoverishment of increasingly isolated islands just as easily; such islands have lower immigration rates for all species.

There have been demurrers, however, of four types, First, Lynch & Johnson (1974) feel that the data on California Channel Island and Karkar birds (Diamond, 1969, 1971) are incomplete and of varying quality. Jones & Diamond (1976) attempt to refute this charge but the dispute reduces to whether one has faith in the completeness of censuses by different workers at different times, and seems irresolvable. Second, Lynch & Johnson (1974), Smith (1975), and Salomonsen (1976) suggest that even were the censuses complete, most observed "turnover" represents transient intrapopulation movement rather than population extinction. There are insufficient data to determine whether this is true, either for the Channel Islands or the Farnes Islands subsequently discussed by Diamond & May (1977). Third, Lynch & Johnson (1974) claim that much turnover of Channel Island birds and those of Mona Island in the West Indies (Terborgh & Faaborg, 1973) is due to anthropogenic habitat change, a claim echoed by Simberloff & Abele (1976) concerning the extinction of birds of Barro Colorado Island (Terborgh, 1974). Jones & Diamond (1976) suggest that 30 % of Channel Island turnover can be attributed to man, but these are all blatant examples, and subtle anthropogenic effects cannot be definitively discounted. I have re-examined the Channel Island data and conclude that four of Diamond's claimed 41 extinctions are unlikely to be due to the above three causes, and another six might well also qualify as real population extinction. These ten are more than the single extinction which Lynch & Johnson (1974) concede, but a far cry from Diamond's 41. This conclusion marches with my re-examination of insect data (Simberloff, 1976): most "extinctions" represented transient movement within populations, but perhaps 10—25 % were population extinctions. For birds as for insects, the critical scarce data are those on the extent to which recruitment is by breeding within the population as opposed to immigration from without.

The fourth objection to the dynamic equilibrium hypothesis is more general. Lack (1971, 1973, 1975) proposed that bird faunas of distant islands are depauperate because distant islands generally have fewer types of resources. Johnson (1975) feels that variation in bird species numbers on mountaintops is also controlled by habitat diversity dif-

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ferences, not shortterm immigration and extinction rates. Equilibrium theory is a ceterus paribus hypothesis, and has always viewed habitat diversity as a critical determinant of species number. In any event, JOHNSON's evidence consists of correlations between species number and many physical factors, but since correlative techniques cannot demonstrate causality, especially when variables like area and habitat diversity are intercorrelated, his data are equivocal. LACK has not performed this sort of analysis, but bases his conclusion on the facts that many mainland birds breed on islands, and most of the remainder are occasionally found there as vagrants. As DIAMOND et. al. (1976) have noted, one cannot infer dispersal ability of one species from that of another, and that vagrants are occasionally found does not impugn the equilibrium hypothesis, which is fundamentally stochastic. Equilibrium theory views immigration rate as monotonically and causally related to colonization probability, so that vagrants on a depauperate distant island represent failed colonizations; higher rates of invasion had the island been nearer would have produced more frequent breeding by any species.

I conclude, then, that dynamic equilibrium theory explains at least part of the geographic distribution of bird species numbers on islands, though the driving turnover rates are considerably lower than those envisioned in the heady days of the theory's infancy, and on near islands population extinction is obscured by transients. The major thrust of research building on equilibrium theory has been a search for the rules, if any, which constrain species composition within the equilibrium species number. Three distinct approaches, two of which antedate equilibrium theory, have been used to try to show statistically that masses of data on distribution and morphology of island birds manifest competitive constraints on coexisting species.

Taxonomic relatedness and competition on islands

ELTON (1946) found that species/genus (S/G) ratios for a number of local plant and animal communities were much lower than those for species lists of large geographic regions, concluding that the difference is caused by "existing or historical effects of competition between species of the same genus, resulting in a strong tendency for species of any genus to be distributed as ecotypes in different habitats, or if not, to be unable to co-exist permanently on the same area of the same habitat." WILLIAMS (1951), using MOREAU's data on bird distribution in 32 East African habitats, quickly demonstrated the S/G difference to be a statistical artifact. If the species in any local habitat were randomly drawn from the entire avifauna, the expected S/G would be lower than that for the entire avifauna, and MOREAU's data showed that there were usually more congeneric pairs and trios (higher S/G) in a habitat than chance would have dictated. WILLIAMS suggested that "if one species in a genus is capable of survival in a given physical environment, it seems likely that other species in the same genus might . . . have a good chance of survival," and that the common physical requirements would override any effects of intense congeneric competition.

HAIRSTON (1964) implied an alternative explanation for WILLIAMS' pattern: that individual species within large genera tend to be less limited ecologically than those in small genera. Such a tendency would lead to a higher island S/G than chance alone would have produced. HAIRSTON asserted that a consideration of monotypic genera

would affirm the relationship between genus size and ecological limitation, but when I examined (SIMBERLOFF, 1970) a number of island avifaunas by randomly drawing subsets of species from their likely mainland source areas, I found exactly WILLIAMS' pattern: slightly higher than expected S/G. Furthermore, removal of all monotypic genera affected neither the trend nor magnitude of the comparison.

GRANT (1966, 1968) erroneously claimed that "ELTON's contention has been questioned by WILLIAMS (1964), but his argument has been refuted by HAIRSTON (1964)." HAIRSTON, of course, recognized ELTON's error, but simply posed an alternative explanation for WILLIAMS' observations, one which turned out not to be supported. GRANT proceeded simply to show that the Tres Marias Islands had lower % congeneric species (lower S/G) than adjacent mainland Mexico. But 3 of these 4 islands had higher S/G than would have been expected for subsets of those sizes drawn randomly from the mainland pool (SIMBERLOFF, 1970). Finally, GRANT (1966) found a monotonic increase in % congeneric bird species vs. area for 18 islands, which he interpreted as resulting from interspecific competition: "Area influences the coexistence of similar species directly (e. g., the effect upon population size) and indirectly (the effect upon variety of food and habitat, which determines the opportunity for ecological segregation and coexistence)." But the correlation between % congeners (or S/G) and area is simply an artifact of the correlations between area and number of species on the one hand, and number of species and % congeners (or S/G) on the other. For several archipelagoes I regressed % congeners (or S/G) on species number, then stepwise added area and other physical variables. For none was there a significant increase in R^2 over that achieved by number of species alone (SIMBERLOFF, 1970).

Finally, COOK (1966) made a related error in his examination of the distribution of bird species numbers in North America. Finding that isopleths of his map of species numbers were very similar to those for his map of the species per family ratio (S/F), with peaks in the same region of Mexico, he sought a competitive explanation: increase in S/F is said to reflect an increase in vertical structure and ecological complexity, allowing related species to coexist more easily by reducing competition. But the similarity of the maps has no biological significance. It is a statistical artifact of the dependence of S/F on species number even for randomly drawn species sets.

Morphological similarity and competition on islands

An apparently disparate literature leads to a second attempt to demonstrate competition on islands by comparing island and mainland birds. This literature has two converging origins. One is the idea of character displacement (BROWN & WILSON, 1956), that allopatric populations of a pair of species resemble one another more than do sympatric populations, presumably because the increased differences reduce competition sufficiently to allow coexistence in the zone of sympatry. GRANT (1972), however, feels that the evidence for most suggested examples of character displacement, including the classic one of Rock Nuthatches (VAURIE, 1951), is inconclusive. Community-wide morphological patterns have also been viewed as resulting from character displacement, on the grounds that minimum size differences are required for similar species to coexist. Constant minimum ratios among size-ranked species of 1.14, 1.2, 1.4, and 2.0 have been claimed for different groups (HUTCHINSON, 1959; SCHOENER, 1965; EMLEN, 1966;

WILSON, 1975; TERBORGH et al., 1978), in each instance the claimed minimum happening to be the minimum ratio for the species set examined.

My colleagues and I (STRONG et al., 1978) attempted to make this statement a testable hypothesis. GRANT (1966, 1968), following SCHOENER (1965), claims that the ratios of bill length (or their % difference) and wing length between related species are larger on islands than mainland because insular competition is more intense, and uses the Tres Marias Islands as an example. For this archipelago we randomly drew the number of species actually found there (in correct family proportions) from a list of birds found in adjacent mainland Mexico, excluding mainland species from habitats not found on the islands. A hundred replicates generated expected ratios of culmen and wing length for the 30 confamilial pairs which are "adjacent" when sizes are ranked. For culmen length 18 of 30 observed ratios and for wing length 14 of 30 observed ratios exceed expectations. By χ^2, biomial, and WILCOXON tests these proportions do not differ from expected. For the California Channel Islands birds and an adjacent mainland pool the result is the same. So bill size and wing length ratios of related island birds may exceed those for mainland communities, but this is also true for random subsets from the mainland communities; competition need not be invoked as an explanation.

For the Galapagos finches, ABBOTT et al. (1977) LACK's contention that differences among island races have evolved because different competitive pressures are generated by different sets of species on each island on which a given finch species is found. Their main evidence is a negative correlation between observed minimum ratios of beak depth and number of *Geospiza* species on an island; supposedly the more intense competition on smaller islands prevents coexistence of birds unless their bills are very different. But expected minimum ratios for randomly drawn subsets from the total Galapagos finch pool are negatively correlated with number of species drawn (STRONG et al., 1978); one can easily intuit that if only two species are present, producing one ratio, it would likely be greater than the minimum of the six ratios produced when four species are present. We find that not only the minima, but none of the ratios are statistically different on the Galapagos than would have been expected had the subsets on each island been random draws from the total pool. We do not claim that the subsets are random, only that the observed ratios do not prove they are not, and certainly provide no evidence for competition.

On the other hand, when for all the Galapagos finches we plot culmen length against a shape parameter (beak depth/culmen length), we get a cluster of island races for each species. We then randomly assembled a community for comparison to a real island community by randomly drawing one subspecies of each species represented on the island, and we found that the mean Euclidean distance for the randomly drawn subsets did not differ statistically from that for the real community. This was true for all 15 islands but San Cristobal, and remained true for transformed data. Again, there was no evidence for community-wide character displacement. However, when we examined bill size and shape independently, a different picture emerged. For each parameter, we ranked each island race within its specific cluster. Rank-sum for each island was compared to expected rank-sum for subsets randomly drawn from the same group of clusters. We found that actual rank-sums tended to be either statistically larger or smaller than expected; that is, finch species sympatric on an island have converged, and have bills more similar in size and/or shape than would a random subset of races of the

same species. This is exactly the opposite of character displacement predicted by interspecific competition, and supports BOWMAN's (1961) claim that the physical characteristics of individual islands, and not interspecific competition, are primarily responsible for finch racial variation.

Assembly rules and competition on islands

Finally, DIAMOND (1975) asserts that the assembly of bird communities on islands follows seven rules:

1. Of all combinations that can be formed from a group of related species, only certain ones exist in nature.
2. Permissible combinations resist invaders that would transform them into forbidden combinations.
3. A combination that is stable on a species-rich island may be unstable on a species-poor island.
4. On a species-poor island, a combination may resist invaders that would be incorporated on a species-rich island.
5. Some pairs of species never coexist.
6. Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination.
7. Some combinations composed entirely of stable sub-combinations are themselves unstable.

Examining data from 141 land bird species on 50 islands in the Bismarck Archipelago, he concludes that these assembly rules can be explained as resulting primarily from interspecific competition, with dispersal differences also playing a role. An examination of these rules (CONNOR & SIMBERLOFF, 1978) was hindered by the fact that the data have never been published and DIAMOND (pers. comm.) has not the time to copy his field notes into a form in which we can use them; we have, however, used the birds of the New Hebrides (MARSHALL & DIAMOND, 1976) and West Indies (BOND, 1971).

For rules 1 and 5, there are 9,870 pairs of birds in the Bismarcks, 1,540 pairs in the New Hebrides, and 22,155 pairs in the West Indies, so it is not surprising that certain ones are not found on the relatively small numbers of islands in these archipelagoes. DIAMOND's 5 examples from the Bismarcks do not constitute a test of whether there are more mutually exclusive pairs, related or not, than chance would dictate were the birds randomly distributed over the islands subject only to the constraints of how many species are found on each island and how many islands each species is found on, plus the limitation of bird species to the sizes of islands on which they are actually found ("incidence ranges"). By simulation we have found the following: For the West Indies, of the 22,155 pairs of birds 12,757 are mutually exclusive, while 12,448 (s. d. = 79) pairs would be expected to be exclusive for randomly distributed birds subject to incidence ranges and the species- and island-total restraints. Of the 1,029 confamilial pairs, 621 are exclusively distributed, while the expected number of a random arrangement would be 437 (s. d. = 18). For the New Hebrides, of the 1,540 pairs of birds 63 are mutually exclusive, while the random expectation is 63.2 (s. d. = 2.9). Of 99 confamilial pairs, 1 is exclusively distributed, while chance would have dictated 1.3 (s. d. = 0.5). There are

27,720 trios of birds in the New Hebrides, of which 3.070 are never found on the same island; the random expectation is 3,068 (s. d. = 105). Of the 304 confamilial trios, 7 are mutually exclusive, and the random expectation is 6.4 (s. d. = 1.9).

In sum, these data show that most or all of the patterns described by rules 1 and 5 are just what one would expect for randomly distributed birds, and competition need not be invoked to explain them. This is not to say that the species are randomly distributed, only that the statistics of the situation do not show nonrandomness. Rule 7 is similar; for example, of 27,720 trios in the New Hebrides, 169 are found on no single island even though each of the three component pairs is found on at least one island. But for birds randomly distributed as described above, one would have expected to find 162.9 such trios (s. d. = 7.2). Rule 6 is untestable since there are no islands in the New Hebrides, West Indies, or Bismarcks with published avifaunas of only two species; consequently there is no way to demonstrate from the biogeographic distributions that any species pair is unstable by itself.

The remaining three rules, at least for the data Diamond presents, are simply consequences of his definitions plus the laws of probability. He defines a "permissible combination" in rule 2 to be one which exists somewhere in the archipelago and a "forbidden" one to be one which does not, but as we have shown, the geographic distributions themselves do not demand an explanation of active resistance for the latter. Nor is there compelling experimental evidence that any combination actively "resists" invasion or is actively forbidden. Diamond claims that five cases directly document active resistance of "forbidden" invaders, but for each one the "proof" rests on an aprioristic "combination" or „compatibility" rule which itself is unproved. In no instance is there evidence of active resistance, unless one begins with the assumption that a distributional gap must be explained by active resistance, in which case we have a tautology.

For rule 3, "stable" and "unstable" are nowhere defined but seem to be used as synonyms for "permissible" and "forbidden", respectively. So the rule becomes: "A combination found on species-rich islands may not be found on species-poor islands." However, any species-rich island contains far more combinations of all sizes than a species-poor island, so by chance alone one would expect to find some combinations on species-rich islands which are found on no species-poor islands. Finally, rule 4 is just a composite of rules 2 and 3 and is as tautological as they.

Conclusion

The assembly rules, just as the literature on S/G ratios and morphological ratios, endeavor to show that island biogeographical distributions manifest interspecific competition, but fail for the same reason as the other attempts. No null hypothesis was posed to suggest what distributions would have been observed in the absence of any deterministic forces. And in all three instances, tests of a properly posed null hypothesis of random colonization fail to falsify it. This is not to say that island colonization is random, only that any competitive interactions are embedded in a welter of other forces and that examination of community-wide biogeographic distributional data is not likely to tease out interactions of a few particular species pairs. Either experiment or very detailed autecological study will be required.

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Reconstructing the Course of Speciation

François Vuilleumier

Introduction

A major goal of zoogeography is to explain the distribution of organisms in time and space. Whatever the level of approach (theoretical, ecological, historical) or the unit of analysis (propagule, species, fauna) selected for research, the basic processes in zoogeography unfold at the level of populations of species: colonization, dispersion, competition, extinction, differentiation, speciation, and adaptive radiation (MacArthur & Wilson, 1967; MacArthur, 1972; Vuilleumier, 1975, 1978).

Because species, as a unit, and speciation, as a process, assume such central roles in evolution (Mayr, 1963) and in zoogeography (MacArthur, 1972), the fundamental methodological problem of historical zoogeography at the species level is how to reconstruct the course of speciation in time and space on the basis of present speciation patterns. Here I shall draw upon selected studies to investigate this problem (further references: Selander, 1971; Meise, 1975; Vuilleumier, 1977).

The description of speciation patterns

Most ornithologists accept the allopatric mode of speciation (Selander, 1971; Vuilleumier, 1976), although specialists of other animal groups interpret speciation by other modes as well (reviews: Bush, 1975; Endler, 1977). In avian biogeography, speciation patterns are described according to the prediction, from allopatric speciation theory, that various stages in the speciation process are discernible in present-day patterns of distribution and differentiation of populations and of species.

These stages correspond to geographical variation between populations of species, geographical isolates within species, and secondary contacts between formerly isolated populations (or species). Mayr (1959, 1963) has championed the study of the population structure of species, emphasizing that geographical isolates can be considered incipient species, and that zones of secondary contact provide a means of evaluating the degree of reproductive isolation. Continent-wide surveys of population structure are Keast's (1961; Australia), Mayr & Short (1970; North America), and Hall & Moreau (1970; Africa).

The description of the population structure of species in terms of isolates, continua (clines and related phenomena), and secondary contacts constitutes, in my opinion, the fundamental datum of speciation analysis in birds and other terrestrial vertebrates. This description contains information on the present-day genetic structure of species (e. g. gene flow between populations estimated through study of clines, isolates, hybrids), and on the current ecological potentialities of species (e. g. relative habitat specialization, ecological obstacles to dispersion, ecological compatibility in sympatry).

But the description of population structure represents only a temporally and spatially fixed universe (the present), and does not contain information that allows one to give

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direct answers to questions about the course of speciation (the past). Today's species are a result of past events, however, so the description of population structure has elements that imply the possibility of reconstructing past speciation.

The differentiation of isolates thus implies that isolation began some time ago; and secondary intergradation (or hybridization) between taxa implies the joining of previously isolated populations that are not yet fully isolated reproductively. However, the fact that isolates are differentiated does not permit one to answer the question of whether isolation was originally due to a break in a formerly continuous distribution, or to a founding event across an already existing gap. Similarly, intergradation between populations does not necessarily imply their former isolation, if, as ENDLER (1977) argues, one cannot easily distinguish primary from secondary intergradation.

The reconstruction of speciation patterns

The investigator searching for an historical explanation usually "imagines" (see MENGEL, 1970) the most likely sequence of events that could have led to the present population structure. In the case of secondary contacts in a continuous ecological zone, for instance, one looks for evidence of past changes in climate and vegetation that might have led, first to isolation, next to expansion and contact (e. g. HAFFER, 1974, for Amazonian forest birds). Where eco-geographical barriers are absent or hard to detect, one looks for extinction patterns to explain the origin of distributional gaps, and for subsequent competitive interactions as likely causal agents in a sequence of speciation (e. g. DIAMOND, 1973, for New Guinea montane forest birds).

Often the supposed past stages of speciation are correlated with the supposed past fluctuations of climate and vegetation during glacial or interglacial episodes of the Pleistocene. Timing and spacing of speciation events may be correlated either rather specifically with particular Pleistocene periods (e. g. MENGEL, 1964, for North American parulids), or more generally with simply glacial or interglacial stages (e. g. VUILLEUMIER, 1969, for high Andean birds.

Examples of continental reconstructions can be found in HALL's (1963) study of the francolins. In several species-groups HALL summarizes a number of stages, including generally an early stage of widespread, continuous distribution, followed by a stage of constriction of range and differentiation in isolation, and eventually by subsequent stages of expansion, contact, and sympatry. Examples of insular reconstructions can be found in BOCK's (1970) discussion of repeated patterns of double invasion, competition, and character displacement in Hawaiian honeycreepers.

In the two quoted reconstructions of speciation patterns and in many others also, one finds thus a postulated sequence of events involving disruption, isolation and differentiation, subsequent contact over a barrier (islands) or not (continents), and eventual sympatry. If such cycles of speciation are repeated, they are sometimes postulated to give rise to complex patterns of insular adaptive radiation (Hawaiian honeycreepers) or to similarly complex patterns of continental sympatry (Amazonian birds; parulid warblers; New Guinea montane forest birds).

These reconstructions are verbal or graphical models of the course of speciation in given taxa or in given faunas. No matter how attractive or suggestive they are, they remain hypothetical. It is interesting to note that most authors mention one sequence of

speciation only (apparently the one that "best fits" the population structure datum), offer no possible alternative sequences, and do not suggest how their model could be tested.

In summary, a literature review exemplified here through a few selected cases, suggests to me that zoogeographers who reconstruct the course of speciation usually adopt, at least implicitly, the following procedural steps:

1. Analyze population structure (sensu Mayr); document geographical isolates and zones of secondary contact through study of museum specimens (to assess variation), mapping of ranges, and field investigation of ecological determinants of variation, isolation, and contacts.

2. Review the literature on Plio-Pleistocene climate and vegetational history (palynological and geological data) of the study area; reconstruct a spatio-temporal sequence of eco-geographical events (e.g. expansion versus reduction of vegetation zones; establishment and collapse of land bridges between islands and mainlands).

3. Correlate postulated eco-geographical events with the postulated course of allopatric speciation in the group under study; identify past barriers that formerly isolated populations; locate refuges where isolation took place.

4. Assign relative or absolute times to various events in the postulated correlated sequences of speciation and Pleistocene history, as a function of the amounts of differentiation of populations.

5. Describe the best fitting speciation sequence.

Assumptions made in reconstructing speciation patterns

Most authors who reconstruct the course of speciation make several assumptions, explicitly or implicitly. Four assumptions stand out especially.

1. The amount (or degree) of morphological differentiation within species (clines, isolates) or between species is generally assumed to be proportional to the amount (or degree) of genetic differentiation. This is probably often the case, but there are exceptions (see Mickevich & Johnson, 1976, and references therein). Another way of examining the above assumption is independently to assume that the amount of genetic differentiation is correlated with sages of speciation, all the way from species populations to full reproductive isolation (e. g. subspecies, semispecies, allospecies, sympatric species). Ayala (1975) found that genetic similarity, measured by an index using isoenzyme data, decreases with increasing stages in speciation. But there are many exceptions, so that it may be unwise at present to state as an experimental result that there is, indeed, a positive correlation between differentiation (genetic and/or morphological) and a given stage in the speciation process. Part of the difficulty here may lie in the possibility that genetic variability sampled by electrophoresis may not reflect the genetic "stages" of divergence (Ayala, 1975).

2. The amount (or degree) of morphological differentiation is generally assumed to be proportional to the time elapsed since divergence started. In other words, subspecies are assumed to be younger than semispecies, and the latter, in turn, younger than allospecies. This may be correct, but there is little supportive evidence. Avise & Ayala (1975) studied genetic divergence (with the genetic distance statistic based on isoen-

zyme data) between two groups of fishes (nine species in nine genera of minnows; ten species of sunfish, *Lepomis*), both of which date back to the Miocene. The mean genetic distances are 0.57 between the taxonomically diverse minnows, and 0.63 between the congeneric *Lepomis*. If one admits the postulate that there is more differentation between genera than between congeneric species, then one would have expected greater divergence between the genera of minnows than between *Lepomis* species, the reverse of AVISE & AYALA's results. It may not be permissible at present to state that there is a positive correlation between differentiation (morphological and/or genetic) and timing of speciation.

3. Competitive exclusion is often assumed to play a paramount role in the distribution of closely related species having recently completed speciation (allospecies). Many parapatric ranges are explained on this basis. DIAMOND's (1973) model of speciation in New Guinea montane forests relies heavily on interspecific competition to account for the altitudinal replacements of congeners along slopes. DIAMOND suggests that "reconstruction of the process of speciation provides [a] test for competition." What DIAMOND appears to say in his paper is that the process of speciation gives evidence that competition is responsible for the observed altitudinal replacements. But since his description of allopatric speciation followed by competition between allospecies is only a postulate, it is not clear how he provided a test for competition. ANDERSON (1977) invented a mathematical model to test the hypothesis that abutting ranges of allospecies and other taxa in secondary contact are maintained by competition. Using data from MAYR & SHORT (1970), ANDERSON finds some evidence that agrees with his model, but also some ambiguous evidence that casts doubt on the general validity of the assumption.

4. Competition resulting in character displacement is often assumed to lead to the establishment of sympatry. But GRANT's (1975) study of the "classical case" of character displacement (*Sitta neumayer* and *S. tephronota* in Iran) leads to inconclusive results about the mechanisms of displacement (see also SELANDER, 1971). Clearly, the assumption does not rest on firm ground. Competitive interactions are also often assumed to be at the root of secondary sympatry patterns during faunal build-up (community evolution; e.g. MACARTHUR, 1972: CODY, 1974; DIAMOND, 1975). Even though such assumptions follow logically from distributional data, and easily lead to mathematical modeling, valid objections have been voiced (e.g. WIENS, 1977).

Discussion

Most speciation in birds and other terrestrial vertebrates is probably allopatric. So the search for spatio-temporal explanations of the existence of isolates and secondary contact zones is legitimate. Zoogeographers construct descriptive models dictated by parsimony or the "best fit" rule, although no, or very few, alternative models are compared to the one offered as the reconstruction of the course of speciation.

Thus the hypotheses given for speciation events in group after group, no matter how convincing, are hard to test. This is due to the lack of factual evidence about the actual spatio-temporal sequences of both vegetation/climate and of avian speciation. One builds inference upon inference, and therefore mixes fact (the datum on population structure) with fiction (the reconstruction of speciation). This difficulty is not restricted to neontological data. Paleontologists have problems interpreting sequences of fossils

through geological strata in terms of allopatric speciation, presumably because the phenomenon of speciation is so rapid geologically speaking that it leaves inadequate traces in the fossil records (Gould & Eldredge, 1977).

We must realize that our reconstructions are fictional. But since science-fiction has often turned out to be true after all, there is no reason to worry too much about the difficulties inherent in reconstructing the past from the present. There is, however, reason for us to look critically at our assumptions and our procedures. We must state other sequences of postulated speciation events as alternatives to the one we believe to be most likely, we must carefully evaluate the significance for avian speciation of studies on other groups in which chromosome and isoenzyme data are added to morphological ones, and we must try alternative methods (e. g. cladistic analysis performed independently of other methodology might permit a test of other hypotheses).

In short, a fresh look at our research protocol in speciation studies is in order. If we understand better the limitations of our data (Endler, 1977) we will define better what questions we can answer when reconstructing the course of speciation. In the meantime, let us admit to ourselves how inadequate our knowledge of the population structure of species is. There is need for long-term, in-depth, research into what I called above the fundamental datum of speciation analysis (I have already made some specific suggestions, cf. my 1977 paper and the one in the symposium on South American speciation, these proceedings).

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Avian Phylogeny and Intercontinental Biogeographic Patterns

Joel Cracraft

Introduction

Biogeography is an historical science and consequently must concern itself with two fundamental aspects of historical analysis, first, the description of the spatial patterns that are the evidence of that history, and second, the causal explanation of those observed patterns. Although it can be argued that both aspects are complexly interrelated, a consideration of each separately facilitates a deeper understanding of biogeographic methodology and of the biological events being studied. Moreover, there is a further rationale for this analytical separation: an observed pattern may have more than one causal explanation. Discussions about historical biogeography have traditionally been characterized by speculation, confusion, and occasionally rancorous debate. Much of this has been scientifically nonproductive and might have been avoided if the questions of pattern analysis and cause had been isolated (Ball, 1975).

It should be evident that both aspects of pattern analysis and causal analysis must be inferred. Neither can be observed. The concept of pattern is theory-laden in that the entities forming a given pattern (in this case, taxa) are subject to definition and recognition, and the emergence of the pattern itself is a consequence of interrelating these entities in term of a chosen theoretical construct, namely our concept of phylogenetic methodology. The concept of causal mechanism is more directly theoretical in that the entire basis for accepting one causal theory over another is dependent on how well each "explains" or is consistent with observational data about pattern.

For over a century it has been a goal of biogeography to seek a unified description of the history of the earth and its biota. This derives from the universally held belief that, in some general way, the biota evolves in response to changes in the spatial relationships of the lands and seas and to changes in climate. In this view, the constituent elements of the biota evolve together, major geological or climatic events thus influencing the evolutionary history of diverse kinds of plants and animals in a parallel manner (Croizat, Nelson & Rosen, 1974). In recent years advances in our unterstanding of earth history and biogeography have done much to reaffirm this expectation of common evolutionary pattern (Cracraft, 1975).

Discussions about avian biogeography traditionally have occupied an uncertain role within the broader problem of general biotic distribution patterns. Thus, it has been claimed frequently that birds, because they are highly mobile, are not easily susceptible to biogeographic analysis and cannot be expected to conform to general distribution patterns shared with fully terrestrial organisms or with fresh-water fishes (Darlington, 1957). As I will attempt to show, this viewpoint is derived in large measure from a failure to separate the two aspects of pattern analysis and process analysis.

The purpose of this paper is to discuss briefly some general methodological principles of biogeographic analysis, to point out some major biogeographic patterns elucidated in recent years, and to show that once proper systematic analyses of avian taxa

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have been undertaken, they can be demonstrated to conform to the distribution patterns shared with other plants and animals.

Theory and method of historical biogeography

We can begin by asking, what do we mean precisely by biogeographic "pattern"? Pattern can be defined as the spatial relationships defined by the distributions of two closely related monophyletic groups. In the narrowest sense there is the spatial pattern of two species descended from a common ancestral species. Early in the history of the two species they will be spatially separated, that is, allopatric; later, they may remain allopatric or they may exhibit spatial overlap to one degree or another. This description can be extended to supraspecific taxa, the only requirement being that the taxa are defined as rigidly monophyletic groups.

If the distributions of monophyletic groups are mapped, patterns or tracks are revealed. These tracks can be hypothesized to represent the distribution of the common ancestor of the taxa under consideration (CROIZAT et al., 1974). That it is essential to map rigidly defined monophyletic groups as illustrated in Figure 1, where two alterna-

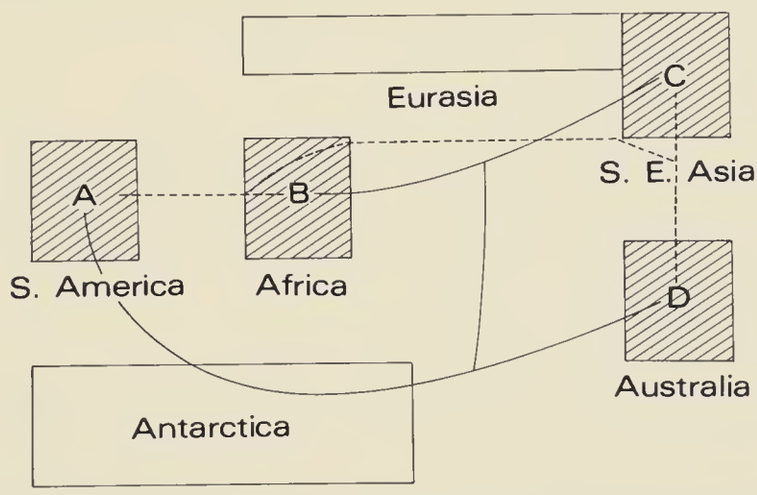

FIGURE 1. Four taxa (A—D) of a monophyletic group are distributed in four areas of Gondwanaland. Tracks (hypothesized ancestral distributions) are drawn based on two alternative phylogenetic hypotheses. First (dotted lines), A and B are sister-groups, as are C and D. A and B are members of the South America—Africa track, C and D of the Southeast Asia—Australia track; the entire distribution is Northern Gondwana. Second (solid lines), A and D are sister-groups, as are B and C. In this case, A and D define a South America—East Antarctica—Australia track, and B and C an Africa—Southest Asia track; the entire distribution encompasses all of Gondwanaland.

tive hypotheses of relationships can produce very different systems of tracks. The example further demonstrates that biogeographic analysis is dependent upon an understanding of the phylogenetic (cladistic) relationships of the taxa, for if the distributional patterns were defined in terms other than strictly genealogical, the biogeographic pattern would be completely misinterpreted (BALL, 1975; CRACRAFT, 1975); moreover, we are interested in discovering pattern using endemic taxa since widespread taxa cannot provide information about vicariance (PLATNICK & NELSON, 1978). Individual tracks, then, are lines connecting the distributions of Hennigian sister-groups.

Generalized tracks are defined when the maps of individual tracks repeatedly overlap one another. It is these generalized tracks of biotic distribution which invite a common causal explanation.

Generalized tracks, because they connect the distributions of sister-groups, can be taken to represent ancestral distributions. What are the causal mechanisms that might establish such ancestral distributions (generalized tracks)? There seem to be only two. The first causal process is vicariance or allopatric speciation in which a barrier is established, thus initiating the separation of the two descendant lineages. That barrier may be of a climatic or geologic nature, arising at some point within the range of the ancestral species, or it may involve large-scale segregation of land masses, thus effectively isolating segments of the ancestral species in two or more fragments of land.

The second causal process is dispersal in which individuals of a species are transported, either instrinsically or by external factors, to another isolated area where differentiation occurs.

How are we to distinguish between the two causal processes in explaining the establishment of any particular generalized track? It is possible to apply a strict interpretation of the criterion of parsimony in which case vicariance would be preferred to dispersal. In this view a generalized track is considered a consequence of a single vicariant event rather than of multiple, independent dispersal events. Furthermore, speciation theory implies that dispersal of descendant lineages should only be invoked if the sister-taxa are sympatric.

But under what circumstances might a generalized track be caused by repeated dispersals of unrelated taxa? The vicariance hypothesis necessarily invokes a geological or climatic event to disrupt a once contiguous ancestral species range. If strong evidence can be presented against such a vicariant event and at the same time for a geographic or climatic situation favoring the merger of two biotas, then a dispersal hypothesis might be preferred (Cracraft, 1975).

Usually, most generalized tracks will signify vicariance. The hypothesis of dispersal is scientifically questionable when the taxa being studied are allopatric. How, after all, is such an hypothesis to be tested? That the organisms have the ability to disperse does not mean that they did; that the organisms are occasionally known to have extralimital occurrences also does not constitute a test of the dispersal hypothesis as applied to a track pattern (Platnick, 1976). Of course, when two sister-taxa are sympatric, that is ipso facto evidence for dispersal. Seemingly, the only test for dispersal is a negative one: the absence of a known vicariant event.

Generalized tracks in the Southern Hemisphere

In recent years, with the accumulation of data on the phylogenetic relationships of diverse taxa, biogeographic analyses have documented a number of generalized tracks in the Southern Hemisphere (Keast, 1972; Cracraft, 1974 a, 1975). Space does not permit extended description, but I will summarize the main tracks and note the generally accepted explanation for each.

Northern Gondwana tracks

There are about five major generalized tracks within northern Gondwana. (1) The South America—Africa track is predominately tropical and involves large numbers of taxa. Almost certainly it represents an ancestral biota vicariated by continental drift in the middle to late Mesozoic. (2) The Madgascar—Africa track is relatively small and

presumably represents a biota isolated by continental fragmentation, although the geological evidence for this remains controversial. (3) The Africa—Eurasia track is rather large und probably constitutes a biota that was continuous prior to late Cenozoic changes in climate separating the two regions. (4) An Africa—Southeast Asia track is comprised of a large number of taxa, and also apparently represents a more or less continuous biota that was fragmented by late Cenozoic climatic and geologic barriers arising from the collision of India and Asia. (5) The Southeast Asia—Australasia track is probably the result of dispersal of faunas as Australia has moved closer to Asia in the Cenozoic. However, many of the individual tracks in this region are surely the result of vicariance as sea levels fluctuated and land masses and island arcs shifted their positions.

Southern Gondwana tracks

There are two well-defined tracks in this region. (1) The South America—West Antarctica—New Zealand track is rather small but well established and undoubtedly evolved as a result of continental fragmentation and drift in the late Mesozoic. (2) The South America—East Antarctica—Australia track is larger than the preceding, also well-documented, and was established by continental fragmentation in the Mesozoic and early Cenozoic.

Track analysis and some avian biogeographic patterns

I now want to attempt a test of the hypothesis that birds, despite what would seem to be their obvious capability for random dispersal, exhibit distributional patterns that conform to the generalized tracks of the world's biota. If the hypothesis is corroborated, then one might reasonably conclude avian distributions have been determined by the same factors influencing the distributions of plants and animals in general.

Tests of this hypothesis rest on our knowledge of the phylogenetic relationships of various avian taxa. At this time such knowledge is not extensive, but it has improved in recent years and is certain to get better in the near future. Evidence supporting the phy-

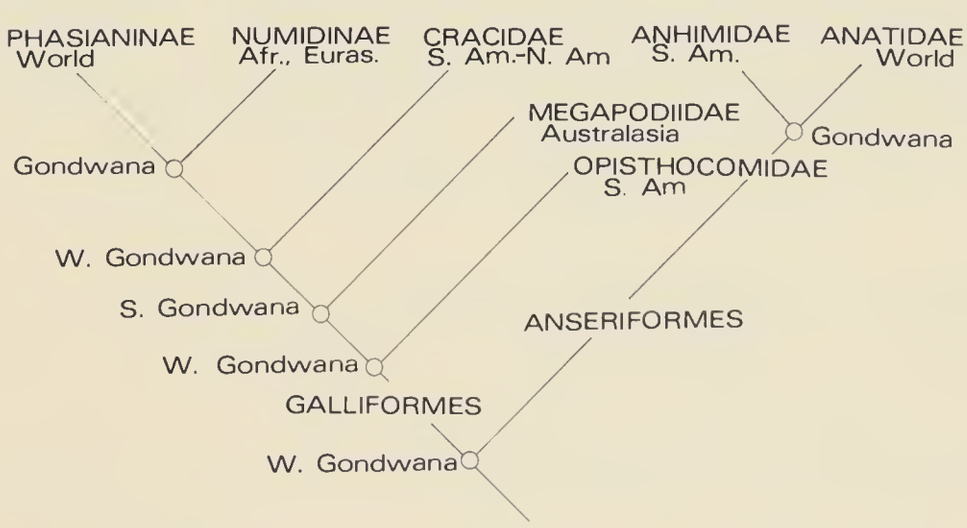

FIGURE 2. An hypothesis of relationships of the Galliformes and Anseriformes showing the hypothesized distributions of ancestral species.

logenetic hypotheses discussed below has been published elsewhere or will be soon. Consequently, I will present only a sample of the best available data relevant to the biogeographic hypothesis noted above. I explicitly emphasize that this sample does not exhaust all the systematic information that might be discussed (see also Cracraft, 1973).

Palaeognathiformes

The phylogenetic relationships of the ratites (Cracraft, 1974 b) suggest membership in most of the major Southern Hemisphere tracks including the South America—Africa track (rheas and ostriches), the South America—West Antarctica—New Zealand track (moas, kiwis), the South America—East Antarctica—Australia track (casowarys, emus), the Africa—Madagascar track (elephant-birds), and the Africa—Eurasia track (ostriches, elephant-birds).

Galliformes—Anseriformes

An hypothesis of relationships is present in Figure 2. There is skeletal and biochemical evidence supporting these relationships, including those of the Opisthocomidae to the Galliformes and the latter to the Anseriformes. Based on these relationships several biogeographic conclusions can be reached. The early history of the two orders was in Southern Gondwana as deduced from the distributions of the Anhimidae, Opisthocomidae, Megapodiidae, and Cracidae. The distributions of the Phasianidae and Anatidae, with their broad sympatry with their sister-groups, have clearly exhibited some dispersal. However, once phylogenetic relationships within these two families are investigated numerous vicariant tracks are certain to emerge. The Megapodiidae would appear to belong to a South America—East Antarctica—Australia track; their membership in the Southeast Asia—Australia track is probably the result of northward dispersal.

Gruiformes

Phylogenetic relationships within a portion of the gruiformes indicate trans-Antarctic distribution patterns (Figure 3). Derived character-states in osteological, myological, and plumage characters support the close relationship of the rhynochetids and eurypygids. Membership in the South America—West Antarctica—New Zealand track is further supported by the close relationship of *Rhinochetus* and *Aptornis* of New Zealand.

Figure 3. An hypothesis of relationships of three families of living Gruiformes showing the hypothesized distribution of ancestral species.

Caprimulgiformes

Figure 4 presents an hypothesis of relationships of the caprimulgiforms based on an analysis of osteological characters. Assuming these relationships, several biogeographic conclusions can be reached. First, the order apparently originated in Gondwana. Second, the aegothelid-podargid lineage belong to the South-America—East Antarctica—Australia track. And third, some members of the Caprimulgidae have shown some dispersal, although once intergeneric relationships are more fully analysed, membership in generalized tracks may become apparent.

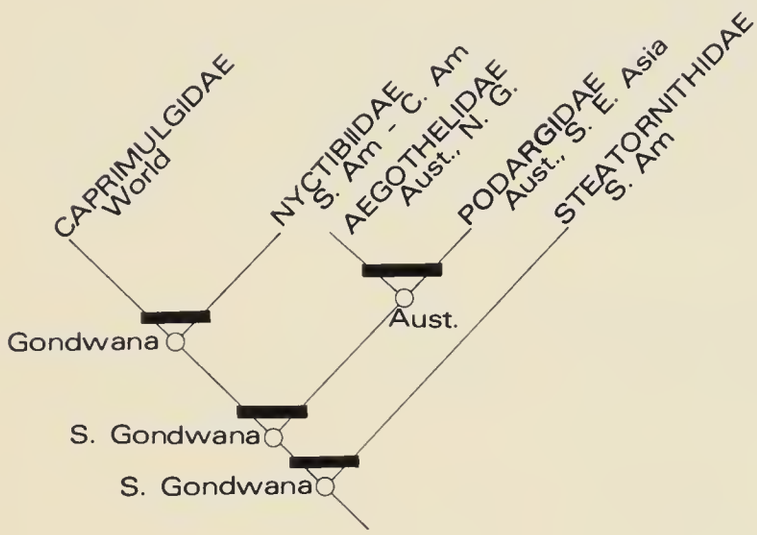

FIGURE 4. An hypothesis of relationships of the Caprimulgiformes showing the hypothesized distributions of ancestral species.

Piciformes

Recent work in my laboratory using osteological data and in that of ROBERT RAIKOW, University of Pittsburgh, using myological data independently support the phylogenetic relationships of the Piciformes shown in Figure 5. This hypothesis indicates the order apparently originated in Northern Gondwana. Although the Primobucconidae are known from the Eocene of North America (FEDUCCIA & MARTIN, 1976), parsimony

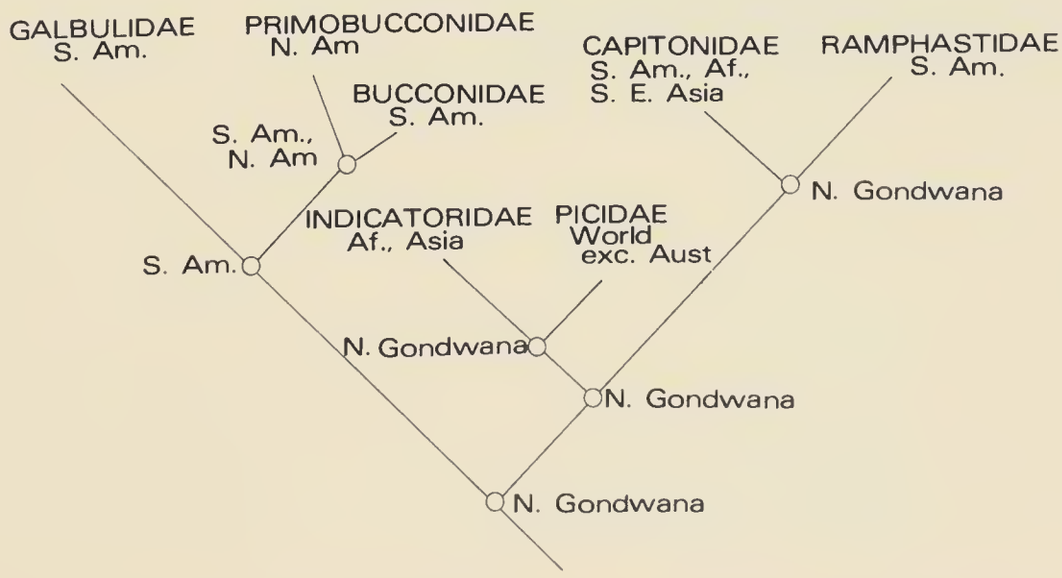

FIGURE 5. An hypothesis of relationships of the Piciformes showing the hypothesized distributions of ancestral species.

would indicate that the common ancestor of the galbulid-bucconid lineage was South American in distribution. Likewise, the common ancestor of the remaining families was also distributed in Northern Gondwana. Once relationships within the Capitonidae and Picidae are better understood, membership in the South America—Africa track probably will be confirmed more strongly than it is now. The worldwide distribution (except Australia) of the Picidae indicates dispersal.

Conclusions

The major thesis of this paper is that the distributional evolution of birds is explicable in terms of the same causal factors which have produced the major distributional patterns observed for the world's biota as a whole. The evidence presented here is consistent with this view. Attempts to refute the hypothesis should focus on showing that inferred ancestral distributions of sister-groups are not individual elements of these generalized tracks.

Acknowledgments

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SYMPOSIUM ON URBANIZATION

9. VI. 1978

CONVENERS: R. K. MURTON AND M. LUNIAK

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Breeding Success and Production of Young in Urban and Rural Woodpigeons in Silesia

Ludwik Tomiałojć

Introduction

The aim of this study was to compare the recruitment indices of the Woodpigeons *Columba palumbus* living under conditions of dramatically different predation pressure though relying on the same, common, food resources of the farmland.

For the purpose of the study two Lower Silesian (SW-Poland) cities were selected, Wroclaw (over 580 thousand inhabitants) and Legnica (c. 90 thousand), both of which have large Woodpigeon populations. For comparison with urban habitats a section of 11.8 km^2 was chosen, situated in farmland surrounding Wroclaw. This plot contains 47.5 ha of woods and village parks, populated with 13–17 pairs of Woodpigeons. Several other sampling areas were scattered over the countryside, providing me with data on population distribution and local density. Some additional data were collected in Bialowieza Primaeval Forest in Eastern Poland.

Method of study

Most census plots were checked according to rules of mapping method census techniques (8–10 visits during the period of the first brood). Special plots – studied more carefully – were checked every 10 days during the whole breeding season, from early April to late September. During each visit the whole plot was checked and by searching each tree I tried to find as many Woodpigeon nests as possible. Nests found and territorial birds were plotted on large-scale maps together with notes on location of nest, behaviour of birds, and, when possible, the number and age of nestlings. Nests were observed by binoculars from below. In spite of this, and thanks to the fixed clutch size, it was possible to estimate the breeding success. The method was almost identical to that used by Stanley Cramp (1972) in central London. Altogether c. 5600 Woodpigeon nests were found. The error in estimating the number of nests in urban parks with few conifers, checked after leaf-fall, did not exceed 5% of the actual number. On the other hand, only 70–80% of nests were discovered in the farmland plot. In this latter habitat, however, it was possible to confirm the existence of some additional successful broods even without finding the nest, from the presence of half-flying fledglings within the boundaries of a known (and in this habitat large) territory.

This method of field work reduced to a minimum the disturbing influence of the observer's presence on the population under study, which can be sometimes quite serious (e. g. Murton 1958).

The number of young fledging per successful nest has been calculated from the sample of 460 nests with known contents. In urban parks free from crows *(Corvus cornix)* the number was 1.8, decreasing to 1.7 when crows were present. In the case of the farmland and some suburban parks the number was only 1.65. The deviation of these figures from

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the clutch size of two is caused mainly by partial predation of nests, as has already been shown by MURTON.

The number of young produced per pair per season was calculated by multiplying the number of successful nests found during the whole breeding season by the number of fledglings in the average successful nest. This sum was then divided by the average number of breeding pairs, derived from two breeding peaks (in late May and late July). Because of the different method of calculation, my figures are slightly lower than the respective figures in MURTON's papers (1958, 1965) and cannot be compared directly.

The results

The Woodpigeon's breeding success in the habitats compared was dramatically different (Figure 1). The difference between central-urban Slowacki Park in Wroclaw (in years without the presence of crows) and suburban Szczytnicki Park or in farmland outside the town, was as much as 6-fold. Generally, it was twice as high in the centre of the town as in the outskirts, showing positive correlation with the intensity of human activity in the town.

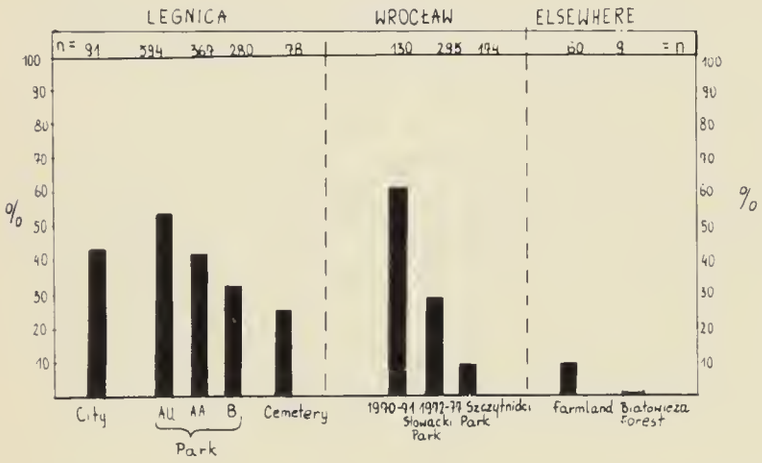

FIGURE 1. Breeding success of Woodpigeons in different areas (data for first broods).

The production of young per pair per season was 3.0–3.49 in the urban parks most frequented by people and only 0.69–0.88 (perhaps sometimes up to 1.0) in the farmland (Figure 2), a 4-fold difference for the whole season and 6-fold for the first brood. The most extreme difference was 27-fold, between central-urban parks (1.08 young/nest/first brood) and farmland (0.04). The production of young per unit area is 175 times higher in central-urban areas than in the nearby farmland.

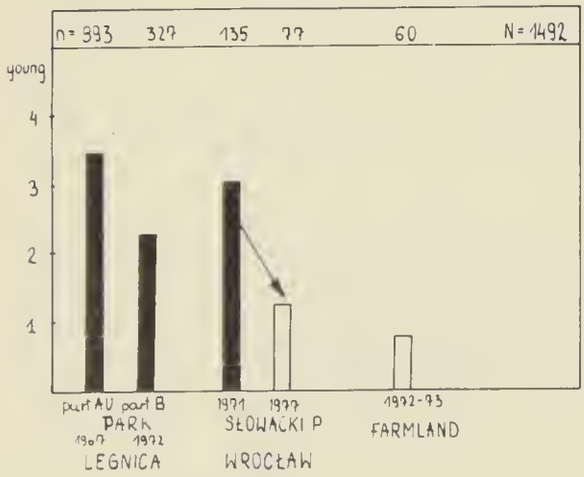

FIGURE 2. Production of Woodpigeon young per pair per season.

Two "natural experiments" were observed. The first one was in the Slowacki Park in Wroclaw, where until 1971 crows were absent. In April 1972 a pair of them started to penetrate the park, since April 1974 crows have bred there every year. The breeding success of Woodpigeons after six years of the presence of crows has decreased by half, and the production of young per pair per season from 3.0 to 1.2. The density of Woodpigeons has also decreased to a half of the previous level (Table 1).

Table 1: Production of young Woodpigeons in Slowacki Park, Wroclaw, in relation to the changing predation pressure of Crows

	Crows absent	Crows visiting		Crows breeding (1 pair)			
	1970–71	1972	1973	1974	1975	1976	1977
Number of pairs in the peaks*	c.48	45	35	35	34	32	27
Number of nests laid in per season	135	146	118	99	114	93	77
Number of successful nests	81	36	49	37	33	26	22
Number of young reared yearly**	c.146	c.63	c.86	c.64	c.56	c.44	c.33
Production of young/pair/season	3.04	1.40	2.45	1.83	1.64	1.47	1.22
Number of young reared per 10 ha	210	90	122	91	80	63	47

* The average from two peaks: in May and July.
** Calculated by multiplying the number of successful nests per empirically estimated average number of young in successful nests. See text.

The reverse change was studied in the Legnica Park, where the density and breeding success have almost doubled after nest predators (smaller corvids and *Strix aluco*) were removed in April 1976. In the next year the Woodpigeon population in the central-town part of this park (part A = 14 ha) reached a density of 220 pairs/10 ha – 440 times higher than in nearby and structurally similar forest.

The fact that there were simultaneous and opposite tendencies in population dynamics in these two towns allows us to exclude the possibility of a coincidental relation between the change in predator numbers and the change in prey population. There are here real causal relations.

Discussion

The results obtained bear on the following more general questions:

(a) the possibility of population control in the Woodpigeon by predation pressure;

(b) the role of dispersal and movements between local populations in regulating the population density;

(c) the nature of synanthropism in birds.

Discussing the first topic, I would like to stress the limitations of the Erringtonian concept of predators acting only as executioners for prey individuals which have been excluded by social mechanisms from the breeding population. This concept can hardly be applied to nest predation, as here we cannot distinctly separate any group of nests or pairs which have been adversely influenced by social mechanisms. The difference in suitability

of particular nest-sites can mostly be seen only post factum through the action of predators, thus being an additional, modificatory, factor to predation. The Woodpigeon populations I studied have shown that there is no upper ceiling set by structural or trophic features of the habitat, or by territorialism, to the density of nests or breeding pairs. This value depends first of all on the kind and number of enemies exploiting the habitat.

Because of sharp differences in reproductive parameters found in my study, and surprisingly high nest mortality in more natural Woodpigeon populations, it seems very probable that nest mortality in this species can play a more important role in population regulation than postbreeding and adult mortality. In primaeval Woodpigeon populations the breeding season mortality (mainly nest mortality) seems to have been of overriding importance, while in overcrowded English populations limited recently by food resources (Murton, Isaacson & Westwood, 1966), and with low nest mortality due to lack of serious predators, the compensatory post-breeding and winter mortality due to food scarcity and via social competition takes the dominant position.

The low effectivity of some predators, claimed for example for English farmland Woodpigeons by Murton & Isaacson (1964), seems to depend on the secondary quantitative incompatibility of prey and predator numbers due to the "safety in numbers" effect (Darwin, 1872; Holling, 1959; Curio, 1976). With the ratio of 215 Woodpigeons to one crow in the farmland at Carlton (East Anglia) the pressure of crows has no serious controlling effect. On the other hand, with the ratio of 1.4 Woodpigeons to one crow in Silesian farmland the effectiveness of predation can be very high, resulting in the destruction of up to 90% of Woodpigeon nests, or even up to 96% during the first brood, when leaf cover is sparse. All 9 first-brood nests studied in the primaeval forest of Bialowieza National Park have also been destroyed or deserted.

The very high production of young by Polish urban Woodpigeons which is occurring without a simultaneous sharp increase in numbers can be eyplained only by heavy emigration of urban young to other habitats and/or other towns. In fact, the exodus of young from several European towns to fields has been recorded (Tomialojć, 1976). On the other hand, the very low production of young in our farmland suggests that this population probably cannot replace itself and depends on immigration from other habitats (urban, and perhaps woodland). This fact indirectly shows the importance of movements (dispersal) of birds between neighbouring local populations. Along with predation pressure this factor seems to play a very important role in determining the local density of Woodpigeons. This makes it very difficult to carry out field experiments, as the natural fluctuations in the neighbourhood can overshadow the results of changes introduced in experimental plots. For this reasion, only experiments carried out in confined ("insular") habitats are likely to give clear answers.

The striking differences in the security of Woodpigeon nests in man-made versus more natural environments suggest that we should modify our views on the nature of synanthropism in birds. This phenomenon has most often been explained on the basis of trophic factors and classified as commensalism. However, the example of the Woodpigeon, a bird that finds security under the "protective umbrella" either of man, or of certain predators *(Falco tinnunculus, Milvus migrans)* or colonial birds *(Corvus frugilegus)* that are highly intolerant of other enemies, indicates that this phenomenon should better be called "protectionism". Of course, in some other species the relationship

with man may be based on both these advantages: better security and better food resources within human settlements.

In the course of their more recent evolution several bird species have liberated themselves from heavy predation by turning to synanthropism. This is why such birds usually have very high hatching success, in the case of Barn Swallow *(Hirundo rustica)* exceeding 83–98%(Vietinghoff-Riesch 1955; Kuźniak, 1967). The same is true of the White Stork *(Ciconia ciconia)*, House Sparrow *(Passer domesticus)* and others. The nesting losses in these species probably only secondarily are caused mainly by scarcity of food, as they now live under conditions of heavy overpopulation, as a result of abatement of predation pressure. By comparing the breeding success (or better, the hatching success) of synanthropic open-nesting Barn Swallows and similarly open-nesting forest populations of other birds, for example Spotted Flycatcher *(Muscicapa striata)* or Chaffinch *(Fringilla coelebs)*, we should be able to evaluate the evolutionary importance of predation pressure, as a cause of bird synanthropism and as a factor in the control of primaeval bird populations.

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Changes in the Breeding Birds of Inner London since 1900

Stanley Cramp

Introduction

Inner London is defined as a rectangular area, 8 miles long by 5 miles wide (c. 102 km^2) centred on Charing Cross. It is not untypical of the centre of a large urban area, with houses, flats, offices, railways, docks and industry, bisected by a large, and until recently, heavily polluted river, but unlike many industrial cities of the 19th century it is blessed with several large parks and many squares (see Cramp & Teagle (1957) for a discussion of the main ecological features). There has been a long tradition of ornithological observation, with markedly increased coverage in recent years. In 1898 the famous naturalist, W. H. Hudson, published a detailed survey of the birds, which, though it recorded some recent colonists, gloomily forecast the steady impoverishment of the avifauna of this central area. The reality has been very different.

Changes in breeding species 1900–75

Species breeding regularly in Inner London (i.e. for at least 4 consecutive years at the dates shown) are listed in Table 1. In the first 25 years the total remained at 25 (though 1 species was lost and 1 gained), in the next 25 years there was an increase of 7 species (with no losses) and from then until 1977 a further increase of 8 species (12 gains and 4 losses). There was thus a net increase of 15 species nesting regularly (60%), of which 6 were non-passerines (an increase of 67%) and 9 passerines (56%).

A further 13 species have bred at irregular intervals between 1900 and 1977. They include 3 non-passerines *(Accipiter nisus, Cuculus canorus* and *Picus viridis)* and 10 passerines. Among the passerines, *Sitta europaea* nested every year from 1958–64 and again in 1976–7, while *Phylloscopus trochilus, Motacilla cinerea* and *M. flava* have all bred on more than 5 occasions, but the remainder *(Hirundo rustica, Sylvia curruca, S. communis, S. borin, P. collybita, R. regulus* and *Carduelis flammea)* have, like the 3 non-passerines, not nested more than twice.

The above summaries exclude one area of Inner London because recent changes there have produced a habitat which is most untypical of an inner city and essentially temporary. This is the old Surrey Docks, in the extreme south-east. Their commercial use ended in the early 1970s and since then they have become largely an overgrown wilderness, closed to the general public. This sanctuary, only 4 km from St Paul's Cathedral, has produced no less than 10 new breeding species for Inner London in recent years – 4 non-passerines *(Alectoris rufa, Charadrius hiaticula, C. dubius,* and *V. vanellus)* and 6 passerines *(Alauda arvensis, Anthus pratensis, Acrocephalus schoenobaenus, A. palustris, Carduelis cannabina* and *Emberiza schoeniclus).* These species are not included in the discussion which follows, but they provide a striking illustration of what can be attracted to an urban area given suitable cover and little disturbance.

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Changes in numbers 1900–75

The increase in the number of regularly breeding species might give a misleading impression of the greater richness and diversity of the avifauna of Inner London if the newcomers were restricted to a pair or two in one favoured habitat. This is not, however, the case. Of the 8 non-passerines which have been gained since 1900, 5 (all waterbirds) have increased in numbers, and spread from their original point of colonization to other parts, while a sixth, *Ardea cinerea*, though still restricted to Regent's Park, has steadily increased. *Falco tinnunculus* which flourished in the bombed areas of the City suffered some decline when these were covered by new buildings but has tended to increase again in recent years. The last, *Larus argentatus*, still breeds in very small numbers, in part, at least, because some of its nests are deliberately destroyed. Of the 11 passerines, again the large majority (8 species) have increased and spread, and all these now appear to be firmly established. The three exceptions are *Phoenicurus ochruros*, *Aegithalos caudatus* and *Certhia familiaris*. The first of these was, even more than *Falco tinnunculus*, helped by the rich vegetation and insect life of the City bombed areas after 1945 (which held for some years the bulk of Britain's breeding population); only odd pairs now nest in Inner London, although the species is now firmly established elsewhere in the London area, especially on industrial sites in the Lea valley and on some power-stations. *Aegithalos caudatus* has declined after a sharp initial increase, and like *Certhia familiaris* its numbers are now so small as to make it highly vulnerable.

In the last 20 years, detailed counts of breeding species have been made regularly in most of the richer areas, including Hyde Park, Kensington Gardens, Regent's Park and the gardens of Buckingham Palace, as well as the squares in Bloomsbury. There is no such precise information for the early years, although W. H. HUDSON's list of seriously threatened species in 1898 included a number which are now firmly established and have often increased and spread, e.g. *Troglodytes troglodytes*, *Prunella modularis*, *Erithacus rubecula*, *Parus major*, *Fringilla coelebs* and *Carduelis chloris* (CRAMP, 1975). For the more abundant species, still less is known, although counts in the Bloomsbury squares 1950–1977 reveal some interesting changes. The decline of *Passer domesticus* has long been noted by many observers and was attributed to the decrease of horse-traffic; the Bloomsbury counts suggest that other factors are now involved, for numbers have fallen by c. 70% since 1950 (when horses had largely vanished from the streets), though they appear to have stabilised in the last 10 years. During the same period, the feral *Columba livia* increased almost 5 times to become Inner London's most numerous bird, although since 1970 there has been some decline. The third most common species, *Columba palumbus*, was much reduced by control measures during the 1939–45 war, increased 5-fold to 1960 and has since declined steadily to about twice the 1950 figure. As all 3 species are largely dependent on bread provided by the public, it seems likely that competition for food between them is now an important factor. The fourth commonest species, *Turdus merula*, has undoubtedly increased greatly since 1900 (as in many other European cities); before 1930 it was largely unknown outside the parks, but is now widespread, having markedly outstripped its relative *Turdus philomelos*.

TABLE 1: Species breeding regularly in inner London since 1900

	1900	1925	1950	1965	1977
Non-passerines					
Tachybaptus ruficollis	B	B	B	–	–
Podiceps cristatus	–	–	–	–	B
Ardea cinerea	–	–	–	–	B
Cygnus olor	B	B	B	B	B
Branta canadensis	–	–	–	B	B
Anas platyrhynchos	B	B	B	B	B
Aythya ferina	–	–	–	B	B
Aythya fuligula	–	B	B	B	B
Falco tinnunculus	–	–	B	B	B
Gallinula chloropus	B	B	B	B	B
Fulica atra	–	–	B	B	B
Larus argentatus	–	–	–	B	B
Columba palumbus	B	B	B	B	B
Columba oenas	–	–	B	–	–
Columba livia	B	B	B	B	B
Apus apus	B	B	B	B	B
Strix aluco	B	B	B	B	B
Dendrocopus major	B	B	B	B	–
Passerines					
Delichon urbica	–	–	–	–	B
Motacilla alba	–	–	B	B	B
Troglodytes troglodytes	B	B	B	B	B
Prunella modularis	B	B	B	B	B
Erithacus rubecula	B	B	B	B	B
Phoenicuros ochruros	–	–	B	B	B
Turdus merula	B	B	B	B	B
Turdus philomelos	B	B	B	B	B
Turdus viscivorus	B	B	B	B	B
Sylvia atricapilla	–	–	–	B	B
Muscicapa striata	B	B	B	B	B
Aegithalos caudatus	–	–	–	–	B
Parus ater	–	–	–	B	B
Parus caeruleus	B	B	B	B	B
Parus major	B	B	B	B	B
Certhia familiaris	–	–	–	–	B
Garrulus glandarius	–	–	B	B	B
Pica pica	–	–	–	–	B
Corvus monedula	B	B	B	B	–
Corvus frugilegus	B	–	–	–	–
Corvus corone	B	B	B	B	B
Sturnus vulgaris	B	B	B	B	B
Passer domesticus	B	B	B	B	B
Fringilla coelebs	B	B	B	B	B
Carduelis chloris	B	B	B	B	B
Carduelis carduelis	–	–	B	B	B
Pyrrhula pyrrhula	–	–	–	B	B
Total: Non-passerines	9	10	13	14	15
Passerines	16	15	19	22	25
Grand total	25	25	32	36	40

Discussion

The avifauna of Inner London, far from declining catastrophically as forecast by HUDSON (1898), has become markedly more diverse since 1900. It is likely that any particular species has been influenced by a complex of factors, but some of the more important of these merit discussion.

Perhaps the major factor has been the change in the public attitude towards birds since 1900. This has been reflected not only in changes in legislation and undertaking of active conservation measures, but, perhaps even more importantly, in the attitude of the general public. The first modern legislation was the Act for the Protection of Seabirds 1869 followed by the more general Wild Birds Protection Act 1880. It is worth remembering that only a hundred years ago many passerines were trapped or limed in the London area, while as late as 1894 people were fined for shooting gulls (presumably *Larus ridibundus*) from London Bridge. For many years now birds have been at no risk from the general public (a few nests are still robbed by small boys); indeed they are encouraged, with large supplies of food, mainly bread, being given to waterbirds and gulls in the parks and to feral *Columba livia, Columba palumbus* and *Passer domesticus* especially in streets and squares. Active conservation measures have also played a major part, especially in recent years. They have been of especial importance in the Royal Parks, where government authorities (advised by the Committee on Bird Sanctuaries in the Royal Parks) have provided sanctuaries for both water-birds and land-birds. The former have had the most obvious effect – ensuring the safety and slow growth of the *Ardea cinerea* colony in Regent's Park, and enabling the recent colonization by *Podiceps cristatus* and the earlier spread and increase of Anatidae and other waterfowl (some species, such as *Fulica atra* and *Aythya fuligula* probably began from introduced eggs or pinioned birds, while the *Branta canadensis* population has developed from the introduction of free-flying birds). The land sanctuaries have had a less dramatic effect, but, as they are closed to the public and provide effective cover, have undoubtedly helped in the increase of species with vulnerable nests. Nest-boxes have been erected in parks, squares, and many private gardens.

These sanctuaries represent the main habitat changes in Inner London during the period, apart from the important but temporary ones caused by bomb damage and the closure of Surrey Docks. The general growth of London almost certainly led to the loss of *Corvus frugilegus* after 1916 as a nesting species by making suitable feeding areas too distant, and may have played a part in the loss of *Corvus monedula.* The loss of old trees, especially of elms *Ulmus* in recent years through Dutch Elm disease, probably led to the disappearance of *Dendrocopus major* as a regular breeding species.

Reduced pollution may have been a factor in recent years. The commendable progress made in cleaning up the Thames has so far had its main effect downstream of Inner London, where there have been marked increases in both ducks and waders (HARRISON & GRANT, 1976). Reduced air pollution, however, seems to have affected several insectivorous species in the central area. The most striking is the return of *Delichon urbica* as a breeding bird after an absence of nearly 80 years; here a correlation was established between the new nesting colonies and the amount of smoke pollution (CRAMP & GOODERS, 1967). There has been some indication also of an increase in the numbers of *Apus apus* (GOODERS, 1969). The possible effects on other insectivorous species were examined by CRAMP (1975), who showed that a comparison of the 17 years before and

after the Clean Air Act of 1956 revealed an increase in the total number of insectivorous species as well as in the numbers of several insect-feeders which had bred regularly throughout. The evidence is, however, circumstantial, as no surveys have been made to determine whether cleaner air has led to an increase in the number and variety of insects.

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Urban Birds in the Context of Canadian Climate and Settlement

Anthony J. Erskine

Introduction

Canada has an area larger than all of Europe (more than six million km^2) with a human population equal to that of the Netherlands and Belgium (about 22 million). Most of Canada is incapable of supporting human settlement at above a subsistence level, even in summer, without importing most of the food and other necessities of civilization. Nearly one-third of Canada is arctic tundra and nearly one-half is subarctic and boreal forests, in which the original inhabitants existed and often perished under a hunter-gatherer subsistence economy. Only a narrow southern strip 200–300 km wide supports agriculture, even today, and 90 per cent of Canada's human population now lives in this southern fringe. Approximately 70 per cent live in cities and towns of 5000 or more inhabitants. The movement of energy into Canadian cities and towns from outside sources to support and employ these people leads to considerable wastage, and birds have been able to exploit this wasted energy.

Major constraints on birds in Canadian cities

A naturalist from Canada visiting more southern cities is impressed by the luxurious vegetation in even new housing developments. Most of Canada has a boreal climate, with severe winters and short growing seasons. Agriculture is generally restricted to the period May through September, and the ground is snow-covered for four or more months each year in most settled areas. Similarly in towns and cities, few tree species are resistant to the cold of boreal regions, and few shrubs can tolerate the deep snow drifts that form around buildings. Growth of trees and shrubs is generally slow, and vegetation is clearly not a dominant cover type in urban areas.

A visitor from a country with a long history would be also struck by the overall newness of Canadian cities and towns. Four hundred years ago the only settlements in Canada were native villages of a few hundred inhabitants, and few of these were occupied year-round. Urbanization occurred only in the last century; urban centres of early periods were linked by water transport and those of the next 50 years were similarly tied to the railway network, but with the evolution of private cars modern cities have sprawled to the horizons. These vast areas of new housing were constructed either on former farmland or on areas from which all trees were cleared, and revegetation of such areas is usually very slow. Even with deliberate landscaping, most new housing areas do not become acceptable to woodland birds until 15 to 20 years after development when the trees have reached heights of 5 to 10 m. Over 60 per cent of Canada's urban area has grown up since 1950, and is occupied by new, single-family houses.

Birds in Canadian cities and towns

The brief time span of urban settlement in Canada has not yet seen the evolution of indigenous urban birds. Most urban bird communities there are dominated by three

Canadian Wildlife Service, Sackville, New Brunswick, Canada

introduced and largely resident species – House Sparrow *(Passer domesticus)*, Starling *(Sturnus vulgaris)*, and feral Rock Dove *(Columba livia)*. An introduced Asiatic starling (*Acridotheres cristatellus)* occupied urban habitats in and around Vancouver from 1900 until it was largely supplanted by the (European) Starling in the 1960s. All these species were pre-adapted to urban niches in Europe or Asia, and were introduced between 1850 and 1900 when cities were first developing in Canada. The most successful native birds in Canadian urban habitats are a large thrush *(Turdus migratorius)*, two American buntings *(Melospiza melodia* and *Spizella passerina)*, a swift *(Chaetura pelagica)* and a goatsucker *(Chordeiles minor)*. Additionally, two icterids, several swallows, four corvids, one parid and one wren are found only in better-vegetated suburban areas, while two woodpeckers, a nuthatch, a creeper, and several cardueline finches frequent cities and towns mainly in winter.

In summary then, our urban birds may be grouped into three main types: (i) introduced residents, largely omnivorous; (ii) native migrants, largely insectivorous and including a number of aerial feeders; (iii) native residents, largely forest or woodland birds, and either trunk/branch gleaners feeding on insects or else nomadic species feeding on tree seeds, but including a few omnivores as well. The second group leaves Canada in winter, while the third generally prefers areas better vegetated than cities or towns in summer (for nesting and rearing young). Except for aerial feeders and the occasional tolerant predator, only the first group occurs in the unvegetated city centres.

Urban bird studies in Canada

The studies summarized in this paper were all made during the last ten years, and most were in the regions with milder winter climates. Several involved year-round counting of birds in selected parts of cities such as Vancouver, Toronto, and Waterloo; others were made in summer or winter only, while generalized data are available for many localities.

Results

Lists of urban birds, mostly with densities, are available from the breeding season for Vancouver, Saskatoon, Waterloo, Toronto, Whitby, Oshawa, Ottawa, and Saint John besides several small towns in the boreal region (Weber, 1972; Lancaster, 1976; J. B. Gollop, unpubl. data; Campbell & Dagg, 1976; J. P. Savard, unpubl. data; Speirs et al., 1969; Erskine, 1977; D. S. Christie, unpubl. data). Winter bird densities are available for Vancouver, Waterloo, Toronto, Ottawa, and some small towns (Weber, 1972; Lancaster, 1976; Campbell et al., 1976; J. P. Savard, unpubl. data; Erskine, 1975).

Discussion

The introduced species (House Sparrow, Starling, Rock Dove) are dominants almost everywhere, making up 70 to 95 per cent or even more of the bird community, but even these vary in response to certain characteristics of the urban areas. The native species show still more pronounced response to such characteristics, which have been described quantitatively by Lancaster (1976) and J. P. Savard (unpubl. ms), and in less detail by Speirs et al. (1969) and Erskine (1975).

The first segregation of data is based on winter climate, as resident species are limited by their ability to survive the winter, when the extent and depth of snow cover severely limits foraging on the ground. Areas studied to date may be grouped thus: (i) largely snow-free in winter – Vancouver (i.e. west coast); (ii) snow cover limited in extent and/or in depth – Toronto, Waterloo, Oshawa (i.e. southern Ontario); (iii) snow cover continuous and usually 30 cm or more in depth for 3+ months – Ottawa, Saskatoon, Saint John, and most towns and cities outside the above-mentioned regions. There is of course no hard dividing line between such groups.

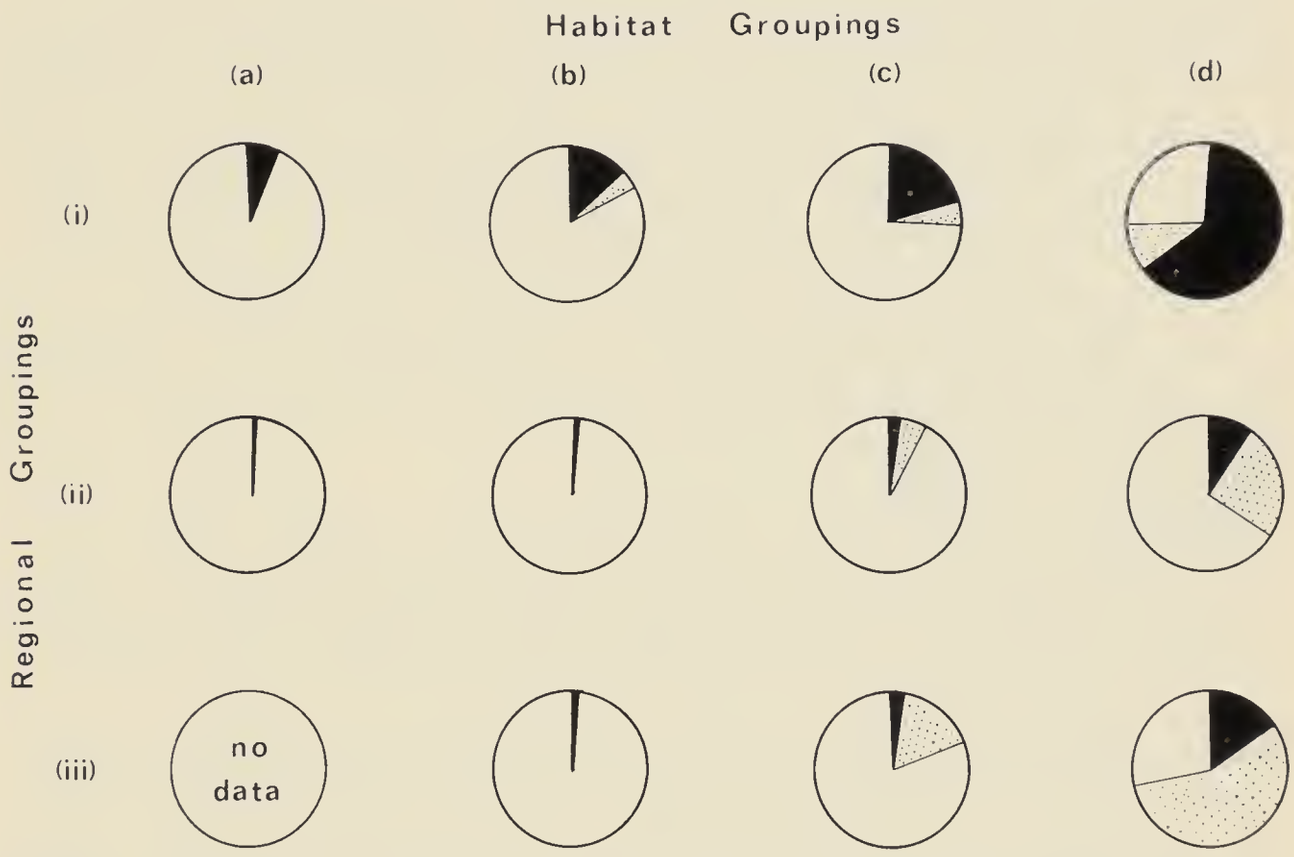

FIGURE 1. Proportions (by density) of introduced residents (white), native residents (black), and erratic species (stippled) among birds in Canadian cities and towns in winter. For regional and habitat groupings, see text.

The second segregation considers types of buildings, which reflect both time since development and also size of the urban area. Groupings represented among studies to date are: (a) commercial and industrial, with little or no vegetation, and no feeding of birds in winter; (b) downtown residential with apartment blocks (large or small) or row housing, vegetation being restricted to narrow strips of lawn and scattered trees, and bird feeding uncommon; (c) suburban residential (the most studied type) with largely single homes, vegetation of limited variety but often occupying 40 to 50 per cent of the area, winter feeding fairly general; (d) estate residential, with large lots, many trees, often with areas of natural undergrowth, and winter feeding general. Not all types were studied in all regions, but all are generally recognizable. Newly built-up areas of suburban housing, with younger and less well-established woody vegetation, fall between (b) and (c), and various other intermediate conditions may be recognized.

The situation is simpler – fewer species of birds, and fewer sources of food – in winter, so this may be considered first (Figure 1). Regional differences are more pronounced in winter, the snowfree west coast cities having abundant bird populations then – as many birds as in summer in some cases. The increased snow cover and lower temperatures elsewhere lead to a decrease in species diversity first, with native resident species (half-hardy birds) disappearing first, but the overall density of birds remains high in the transition zone of southern Ontario. In the snow zone proper, total densities as well as diversities dwindle in progressively colder areas, but the nomadic species of the boreal region (carduelines, waxwings) become relatively more important.

In the west coast cities in winter, Starlings generally outnumber House Sparrows in all habitat types, in contrast to all other areas studied to date. Two possible explanations come to mind. Starlings only reached the west coast during the last 25 years, having spread across the continent from introductions in the east. Most introduced birds exhibit a rapid build-up in numbers followed by a decrease to some lower equilibrium population level, so it is possible that Starling density will decline in future in these west coast areas. Alternatively, and more probably, in winter most Starlings leave the Canadian prairies and probably up to half the population leaves southern Ontario, so areas in the snow zone have relatively lower Starling densities in winter. In contrast, substantial numbers of Starlings from the British Columbia interior winter in and around Vancouver, which thus has relatively higher densities than cities in the snow zone.

Considering now the different urban habitats, the numbers of species found in winter increase from (a) to (d), roughly paralleling the increase in vegetation. The density, however, falls from (b) to (d), with (a) having the lowest of all, almost entirely of the introduced species with a few native omnivorous scavengers like gulls and crows (Figure 1). The decreasing density from (b) to (d) reflects changes in densities of the introduced species, which prefer open, treeless areas for foraging, and large, older buildings – as in (b) – with more ledges and openings for safe roosting places. The increasing diversity in turn reflects the numbers of native species, which in winter are largely dependent on trees. There is a further correlation here, in that higher tree densities on private property generally reflect higher incomes; so the more wooded residential areas also contain higher densities of bird feeding stations, which cater preferentially to native birds, whereas urban feeders tend to be overrun by the introduced species.

In summer, with the return of deciduous foliage and disappearance of snow cover, there is less difference in the variety of niches for birds between the regions. The differences that exist probably reflect in part the nature of the original vegetation of the regions, as areas with broad-leafed trees receive annual litter enrichment through leaf fall, which is greatly reduced in areas dominated by conifers. Southern Ontario, which was originally covered by broad-leafed woodland, shows somewhat higher bird diversity than either the west coast or more boreal areas, where conifers were more important in the forests, though the differences are slight.

For the different urban habitats (Figure 2), the diversity pattern is similar to that in winter, increasing from (a) to (d), though the last is less distinct from (c) than in winter. There is no clear pattern for relative total densities except that (a) is again the lowest, with the introduced species almost alone and in relatively low densities, as would be expected from the scarcity of feeding opportunities. In summer, the increased densities of native

species almost balance out the decreasing densities of introduced birds as one goes from (b) to (d), as the more wooded areas can then support migrant insectivores as well as the native resident bark-gleaners.

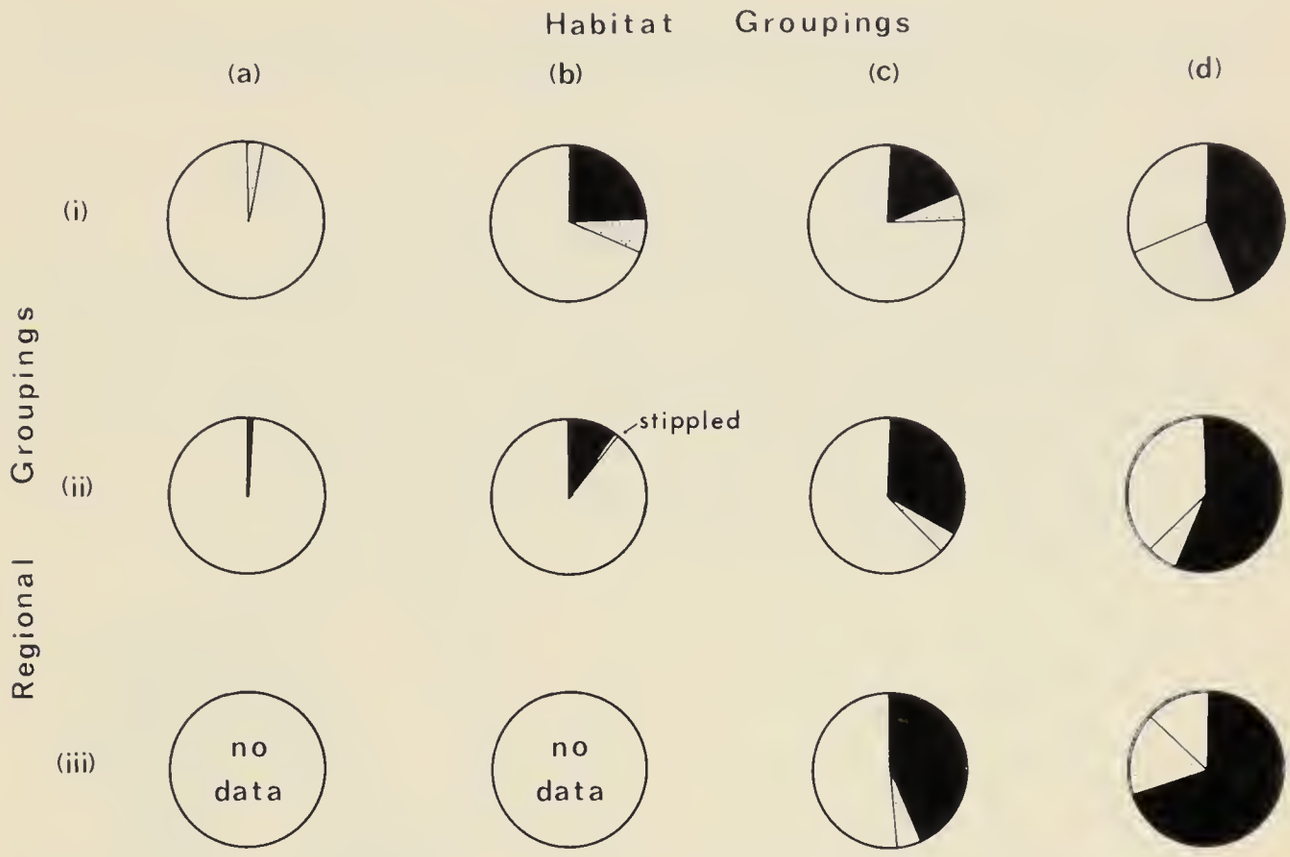

FIGURE 2. Proportions (by density) of introduced residents (white), native migrants (black), and native residents (stippled) among birds in Canadian cities and towns in summer. For regional and habitat groupings, see text.

In general, the patterns of distribution and density found among Canadian urban birds are quite predictable from even the limited data now available, and they offer few surprises. Most native species have not yet learned to exploit wastage from human translocation of energy (food, heat, etc.) into urban areas, so must still depend on more or less natural vegetation. In contrast, the introduced species were pre-adapted to cities, and nest in well-protected sites. They were also to a considerable extent scavengers, and perhaps because they thus performed a public service in days before garbage collection, these birds were not hunted in America whereas native scavengers (crows, gulls) were and sometimes still are treated as "bad birds", so have seldom been allowed to nest in urban areas in America; this is changing slowly. Species that exploit buildings as nesting substrates are better adapted for urban life than others, as ground nesters are almost lacking and tree and shrub nesters quite restricted. Most urban birds, except the aerial feeders with their long nestling periods, raise two or more broods annually, taking advantage of the warmer microclimate to start earlier, and of the frequently ample food supplies, but seasonality of breeding is almost inevitable in the Canadian climate. City planners have been slow to recognize birds as desirable, since to most people urban birds means the introduced "feathered rats". With the increasing knowledge of urban ecology we are now better able to show how to improve urban life for people and birds at the same time.

Acknowledgements

I wish to acknowledge the efforts of the symposium organizers, Drs. Luniak and Murton, without which I would probably not have undertaken this review at this time, and of the Canadian Wildlife Service, which has supported my urban bird studies throughout. I also acknowledge the work of Wayne Weber, Richard Lancaster, and especially Jean-Pierre Savard, on whose unpublished theses I have drawn heavily to supplement my own studies and those already published by others.

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Some Problems of Conserving Birds in an Urban Area

L. A. Batten

The study area is located 6–7 miles (10–12 km) northwest of Marble Arch in London, and covers 817 ha. During the last 100 years it has become 70% urbanised, and now consists of a mosaic of habitats, including houses and factories, parkland, playing fields, scrub and woodland, allotments, open water and reed swamp. There has always been at least one ornithologist working in the area during the period of urbanisation, and from their records it has been possible to measure the decrease in breeding species with increasing urbanisation. The number of species breeding when the area was rural was 77 but decreased to 68 when the area was 10% urbanised, 66 at 30%, 63 at 50% and 53 at 70%. In the fully urbanised part of the study plot only 21 species now breed. Details of the species lost can be found in Batten (1972).

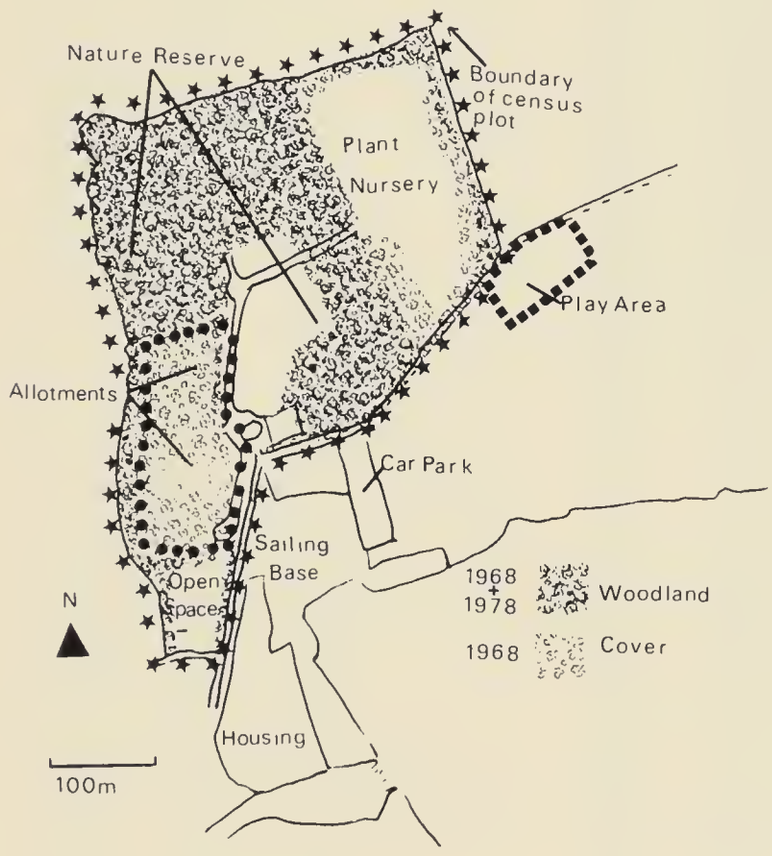

Figure 1. Final amentiy plan an loss of woodland cover for the woodland and scrub plot.

Any further urbanisation seems likely to result in more marked decreases in the number of breeding species. Since 1968 breeding bird census work has been carried out to determine the relative importance of the different habitats still to be found in the study plot. Details of the mapping method used can be found in Williamson & Homes (1964). The 9.7 ha of undisturbed scrub and woodland near the reservoir was particularly rich and so was the reed swamp at the eastern end of the reservoir. Unfortunately both these sites were threatened with housing development.

Nature Conservancy Council, 19 Belgrave Square, London S.W.1, UK.

TABLE 1: The scrubland census results before, during and after the change in land use.

Species	1968–70 average No. of territories	1968–70 % dominance	1971–74 average No. of territories	1971–74 % dominance	1975–77 average No. of territories	1975–77 % dominance
Mallard *Anas platyrhynchos*	0.3	0.2	0.0	0.0	0.3	0.2
Kestrel *Falco tinnunculus*	0.7	0.3	0.3	0.2	0.3	0.2
Pheasant *Phasianus colchicus*	0.3	0.2	0.3	0.2	0.0	0.0
Collared Dove *Streptopelia decaocto*	0.0	0.0	0.0	0.0	0.3	0.2
Cuckoo *Culculus canorus*	0.3	0.2	0.0	0.0	0.0	0.0
Tawny Owl *Strix aluco*	1.0	0.5	1.0	0.6	0.3	0.2
Crow *Corvus corone*	1.7	0.9	2.3	1.3	2.7	1.7
Magpie *Pica pica*	1.3	0.7	2.3	1.3	3.0	1.9
Jay *Garrulus glandarius*	1.0	0.5	1.3	0.7	2.7	1.7
Great Tit *Parus major*	11.7	6.0	12.0	6.7	13.0	8.2
Blue Tit *Parus caeruleus*	16.3	8.4	16.5	9.2	15.0	9.5
Coal Tit *Parus ater*	1.0	0.5	0.5	0.3	0.7	0.4
Willow Tit *Parus montanus*	1.7	0.9	1.3	0.7	1.0	0.6
Long-tailed Tit *Aegithalos caudatus*	0.0	0.0	0.3	0.2	0.3	0.2
Wren *Troglodytes troglodytes*	14.3	7.4	16.8	9.3	14.3	9.1
Mistle Trush *Turdus viscivorus*	0.3	0.2	0.0	0.0	0.3	0.2
Song Thrush *Turdus philomelos*	17.3	8.9	16.0	8.9	11.3	7.2
Blackbird *Turdus merula*	37.0	19.0	31.0	17.3	26.7	16.9
Robin *Erithacus rubecula*	24.7	12.7	25.8	14.4	22.0	13.9
Blackcap *Sylvia atricapilla*	4.0	2.1	3.8	2.1	2.7	1.7
Garden Warbler *Sylvia borin*	1.3	0.7	0.0	0.0	0.0	0.0
Whitethroat *Sylvia communis*	3.0	1.5	0.5	0.3	0.7	0.4
Lesser Whitethroat *Sylvia curruca*	1.7	0.9	2.5	1.4	0.7	0.4
Willow Warbler *Phylloscopus trochilus*	7.3	3.8	6.3	3.5	3.7	2.3
Chiffchaff *Phylloscopus collybita*	1.0	0.5	1.5	0.8	0.7	0.4
Spotted Flycatcher *Muscicapa striata*	0.3	0.2	0.0	0.0	0.0	0.0
Dunnock *Prunella modularis*	23.3	12.0	20.0	11.1	19.0	12.0
Pied Wagtail *Motacilla alba*	0.0	0.0	0.0	0.0	1.0	0.6
Greenfinch *Carduelis chloris*	9.7	5.0	9.0	5.0	5.3	3.4
Goldfinch *Carduelis carduelis*	2.0	1.0	1.5	0.8	2.3	1.5
Linnet *Acanthis cannabina*	0.3	0.2	0.8	0.4	1.7	1.1
Lesser Redpoll *Acanthis flammea*	0.3	0.2	0.5	0.3	0.0	0.0
Bullfinch *Pyrrhula pyrrhula*	5.0	2.6	5.3	2.9	4.3	2.7
Chaffinch *Fringilla coelebs*	2.0	1.0	0.3	0.2	0.7	0.4
Yellowhammer *Emberiza citrinella*	1.3	0.7	0.0	0.0	0.3	0.2
Reed Bunting *Emberiza schoeniclus*	0.7	0.3	0.5	0.3	0.0	0.0
Tree Sparrow *Passer montanus*	0.0	0.0	0.0	0.0	0.7	0.4
Total number of territories	194.1		180.2		158.0	
Total number of Species	33		28		31	

An alternative plan for making the scrub and woodland plot into a fieldcentre for the use of schools was placed before the local Council. This plan resulted in the housing development being scrapped, but an amenity plan for the site was put forward by the local Council. This involved an adventure play area, riding stables, car park, sports field, a plant

TABLE 2: The marshland census results before and after the reservoir was temporarily drained.

Species	1970–72 average No. of territories	1970–72 % dominance	1975–77 average No. of territories	1975–77 % dominance
Great Crested Grebe. *Podiceps cristatus*	1.0	1.2	10.3	5.1
Little Grebe *Tachybaptus ruficollis*	0.3	0.4	5.7	2.8
Mallard *Anas platyrhynchos*	5.0	5.0	13.3	6.6
Gadwall *Anas strepera*	0.0	0.0	0.7	0.3
Tufted Duck *Aythya fuligula*	1.7	2.0	4.0	2.0
Pochard *Aythya ferina*	0.0	0.0	1.0	0.5
Mute Swan *Cygnus olor*	0.3	0.4	1.0	0.5
Moorhen *Gallinula chloropus*	4.0	4.7	12.7	6.3
Coot *Fulica atra*	0.7	8.3	22.7	11.2
Kestrel *Falco tinnunculus*	0.0	0.0	0.3	0.1
Skylark *Alauda arvensis*	0.7	0.8	1.0	0.5
Crow *Corvus corone*	0.7	0.8	1.3	0.6
Magpie *Pica pica*	1.0	1.2	1.0	0.5
Jay *Garrulus glandarius*	0.0	0.0	1.3	0.6
Great Tit *Parus major*	2.7	3.2	4.0	2.0
Blue Tit *Parus caeruleus*	3.3	3.9	10.3	5.1
Wren *Troglodytes troglodytes*	8.3	9.8	19.3	9.5
Song Thrush *Turdus philomelos*	6.7	7.9	9.3	4.6
Blackbird *Turdus merula*	13.3	15.7	14.3	7.1
Robin *Erithacus rubecula*	5.0	5.9	9.0	4.4
Reed Warbler *Acrocephalus scirpaceus*	2.7	3.2	10.3	5.1
Sedge Warbler *Acrocephalus schoenobaenus*	2.7	3.2	10.0	4.9
Blackcap *Sylvia atricapilla*	0.0	0.0	1.7	0.8
Lesser Whitethroat *Sylvia curruca*	0.3	0.4	0.0	0.0
Willow Warbler *Phylloscopus trochilus*	0.3	0.4	3.3	1.6
Grasshopper Warbler *Locustella naevia*	0.3	0.4	0.0	0.0
Dunnock *Prunella modularis*	7.7	9.1	15.7	7.8
Pied Wagtail *Motacilla alba*	1.0	1.2	0.3	0.1
Goldfinch *Carduelis carduelis*	0.0	0.0	2.7	1.3
Greenfinch *Carduelis chloris*	2.7	3.2	1.7	0.8
Linnet *Acanthis cannabina*	0.3	0.4	1.3	0.6
Bullfinch *Pyrrhula pyrrhula*	1.0	1.2	2.0	1.0
Reed Bunting *Emberiza schoeniclus*	4.7	5.5	10.7	5.3
Tree Sparrow *Passer montanus*	0.0	0.0	0.3	0.1
Total number of territories	84.7		202.5	
Total number of species	27		32	

nursery, some housing and a nature reserve. This plan would have resulted in only 3 ha of scrubland and woodland out of the original 9.7 remaining intact. Because of this and other threats to the natural history interest of the area a conservation group was formed which consisted of four local authority councillors and representatives of local environmental interests. The group discussed plans to accommodate the main needs in a way which lessened considerably the environmental impact and left more of the woodland intact. The

plan finally adopted by the local authority is shown in Figure 1. It resulted in a loss of 35% of the woodland cover. This was 5% greater than expected due to several mistakes by the workforce with their bulldozers and individual officers not following the plan, and demonstrated the importance of being present on a site when work of this nature is being carried out.

Bird census work was carried out on the site to monitor the effects of the changes in land use which took place between 1971–74. The results are given in Table 1. *Columba palumbus, Sturnus vulgaris* and *Passer domesticus* have been excluded from the census, as they are not amenable to accurate censusing by this technique. Despite the loss of woodland shown in Figure 1 and up to 100 school children using the site most days, there was only an 18.6% loss in the number of territories detected, and a reduction of two breeding species. This figure resulted from a loss of six irregularly breeding species and a gain of four new species. The regularly breeding species which decreased most were *Strix aluco* as a result of Dutch Elm disease, *Turdus merula, Turdus philomelos, Parus montanus, Emberiza citrinella, Fringilla coelebs* and most of the warblers. The decrease in *Sylvia communis* reflected the national situation and was thought to be due to a drought in its African wintering grounds (Winstanley et al., 1974). In contrast the Corvidae increased, whilst *Motacilla alba* started to nest in the greenhouses of the plant nursery. The increase in the population of *Acanthis cannabina* may have been related to the new allotments.

At the same time the marshland of the eastern end of the reservoir was threatened by a proposed development of a block of flats close to the water's edge. A plan for a boating lake near the marsh was dropped after discussions with the local authority, but the proposals by the British Water Board to build flats on their land close to the reservoir remained firm. It took a public enquiry in 1974 to have them moved further away from the water. The report of the inspector contained a statement to the effect that no development of any kind should take place closer to the water's edge than the nearest of the existing houses.

In 1974 the reservoir had to be drained for the summer to enable important repair work to be carried out on the wall of the dam. This resulted in an extensive increase in the emergent vegetation which formed an effective buffer zone between the new estate and the marsh. Breeding bird census results are given in Table 2. They revealed that the number of pairs increased by a factor of 2.4, and five new species started to hold territory, including *Anas strepera* and *Aythya ferina*. Large increases were noted in most species, particularly *Aythya fuligula, Podiceps cristatus, Tachybaptus ruficollis, Fulica atra, Gallinula chloropus, Acrocephalus scirpaceus, Acrocephalus schoenobaenus* and *Emberiza schoeniclus*. The area also became a much more effective refuge for waterfowl during the winter, when sailing activities took place on the reservoir (Batten, 1977). The changes which took place in the vegetation as a result of the temporary drainage produced beneficial effects far greater than anything the conservation group could have achieved in the short term.

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Local Movements of Starlings in Winter

Christopher J. Feare

Introduction

Winter flocks of Starlings *(Sturnus vulgaris)* frequently feed in close association with domestic stock and considerable losses of cattle food have been demonstrated (Besser et al., 1968; Feare & Swannack, 1978). Starlings also feed at, among other places, sewage treatment plants, rubbish tips and bird tables and this has led to concern at the possibility of their transmitting disease (especially Salmonellae), from farm to farm, from waste disposal sites to farms, and from either of these feeding areas to domestic gardens. The following study was designed to assess the feasibility of pathogen transfer by Starlings through an investigation of the local movements of marked individuals. The population consisted largely of migrant Starlings from continental Europe (Feare, 1975).

Methods

The study area comprised two sewage treatment plants serving the City of Winchester, England, and a nearby farm, Bridgets Experimental Husbandry Farm. Starlings that fed at these three sites, and also within the city, roosted together at night in a roost (in 1976–7 two roosts were occasionally used simultaneously) the position of which varied during each winter. The roost was never more than 10 km from the feeding areas considered here, and the two sewage treatment plants and the study farm were each about 5 km apart (Fig. 1). As the appearance of Starlings at the sewage treatment plants was irregular the marking programme was concentrated at the farm, and experience gained early in the study indicated that the subsequent searches for marked birds should be concentrated there.

Starlings were caught in mist nets in an indoor calf feeding unit at the farm. They were banded and given plastic coated nylon ("Saflag") wing tags bearing individually identifiable colour codes: using a 20 x telescope the colour codes could the recognised up to c. 200 m.

Table 1: The proportion of males in samples of Starlings caught in mist nets at the calf unit, the mean number of Starlings counted from the road transect round the farm, and the mean number of birds in flocks of Starlings that fed in the calf unit. The mean numbers of Starlings on the farm and feeding in the calf unit were obtained from counts made in December, January and February, avoiding the main times of arrival and departure of migrants.

Year	% males (n)	no. of birds counted on farm transect ± s.e.	flock size of birds feeding in calf unit ± s.e.
1975–6	68.6 (121)	769.4 ± 27.2	97.7 ± 6.7
1976–7	77.1 (131)	1150.1 ± 76.6	168.9 ± 15.0
1977–8	66.7 (36)	915.8 ± 68.6	58.3 ± 4.3

Ministry of Agriculture, Fisheries and Food, Pest Infestation Control Laboratory, Field Research Station, Tangley Place, Worplesdon, Guildford, Surrey GU3 3LQ, UK.

Marked birds were subsequently searched for from a standard road transect around the farm and the farm buildings (Feare, 1975) and (1977–8) at the sewage treatment plants. In addition, local bird-watchers were asked to report any tagged birds that they saw. The farm searches were undertaken throughout the daylight hours on two or three days each week from early December to early March – the duration of the migrant birds' winter residence. The activity (feeding, sitting, roosting etc.) and location (building or code names for fields or clumps of trees) of each marked Starling were recorded. The differential visibility of tagged birds in different situations led to bias in the results which restricted the analyses that could be undertaken. For example while tagged birds that were feeding in grass fields could be readily seen and identified, birds feeding in buildings were often hidden by walls, cattle or other birds. These birds could usually be identified only when they were driven out of the building by the observers, and then only if they settled in nearby trees or fields; some individuals were inevitably not identified. Thus sightings of birds in the farm buildings tended to under-represent their occurrence there. However, in view of the large number of sightings of tagged birds in and around the farm, compared with the numbers seen elsewhere, these biases are thought unlikely to have significantly affected the results of the analysis undertaken below. In particular, there was no bias in the relative visibility of males and females.

On one day each week all Starling flocks encountered on the road transect around the farm were counted or estimated (depending on size and mobility). During the course of the day at least three such transects were made (Feare, 1975), and at approximately hourly intervals throughout the day the number of birds feeding in the calf unit was also estimated.

Figure 1. The study area and positions of sightings of wing-tagged Starlings. The dotted line encloses the area around Bridgets E.H.F. regularly searched for marked birds, and the arrow the site at the farm where the birds were caught. Solid circles are the two sewage treatment plants and stars are the roosts used at various times during this study.

Results

The samples of Starlings caught at the calf unit contained a high proportion of males (Table 1) in the three winters of this study. Significantly more birds were present on the farm in 1976–7 than in 1975–6 ($t = 5.50$, $df = 78$, $p < 0.001$), and this was reflected in a significantly larger flock of Starlings utilizing the calf unit in 1976–7 ($t = 4.98$, $df = 128$, $p < 0.001$) (Table 1). Although in 1977–8 the number of Starlings present on the farm was intermediate between the two previous winters, and not significantly different from either of them, the size of flocks feeding in the calf unit was significantly lower than even the 1975–6 figure ($t = 4.76$, $df = 171$, $p < 0.001$): this resulted in the catching of only a small sample of birds for marking in 1977–8 and was thought to be due to unusually severe human disturbance during the construction of new buildings.

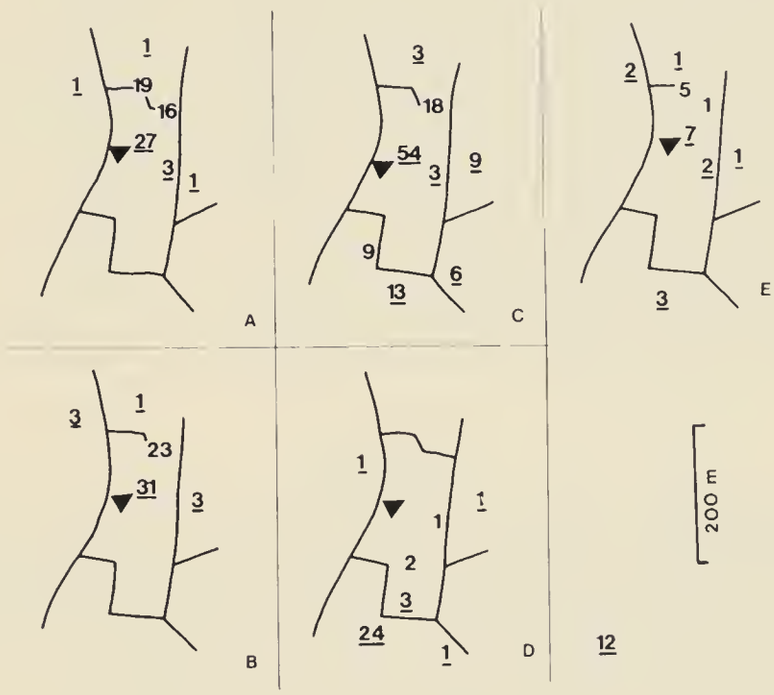

FIGURE 2. The positions of sightings of some individual Starlings. Arows indicate the site of marking and release, underlined figures refer to feeding birds and figures not underlined refer to birds roosting during the day.

Few tagged Starlings were recorded, either by observers or by the public, away from the immediate vicinity of the marking site (Fig. 1) and none were seen at the sewage treatment plants. This suggests that the marked birds returned daily from the night roost to the same feeding areas. This fidelity to a feeding area was confirmed by the sightings of individual birds (Fig. 2): they not only repeatedly fed in the same place (same building or even same corner of a field) but also repeatedly used the same branches of trees as daytime resting sites. Despite this fidelity to preferred sites, birds that had been caught at the calf feeding unit were observed feeding elsewhere on the farm (Fig. 2). However, over 95% of sightings of feeding birds (except for females in 1977–8, where the sample was very small) were within 400 m of the marking site (Table 2) and the distribution of sightings of males and females within this distance showed annual differences. In 1975–6 and 1976–7 the distributions of males and females were significantly different ($X^2 = 17.7$, $p < 0.01$; $X^2 = 13.1$, $p < 0.05$ respectively), but while in 1975–6 the females were feeding closer to the calf

unit than the males, the reverse occurred in 1976–7. A comparison of the distribution of males in the two winters showed no significant difference ($X^2 = 2.71$, $0.5 > p > 0.3$), but the difference between females for the two years ($X^2 = 26.74$, $p < 0.001$) indicated that females tended to feed further away from the farm in 1976–7 than they did in 1975–6. In 1977–8 too few females were caught, marked and subsequently seen to justify analysis, but males fed further from the calf unit than in the previous two winters (for 1975–6 and 1977–8: $X^2 = 12.0$, $p < 0.01$).

Table 2: Distribution of sightings of feeding wing-tagged Starlings within 400 m of the calf unit where the birds were initially caught.

		% of sightings in 100 m intervals				% of all sightings within 400 m	total sightings
		0–100	100–200	200–300	300–400		
1975–6	♂	69.2	12.3	16.7	0.0	98.2	611
	♀	87.2	11.1	0.6	0.6	99.4	180
1976–7	♂	70.8	13.0	10.3	1.2	95.3	339
	♀	53.4	25.2	7.8	8.7	95.1	103
1977–8	♂	50.0	31.4	14.4	0.4	95.4	197
	♀	46.2	0.0	53.8	0.0	38.2	34

Discussion

Most Starling populations contain an excess of males (Coulson, 1960). However, the proportion of males found in samples netted at the calf unit equalled or exceeded those found in samples obtained at roosts (Coulson, 1960), suggesting that males were selectively feeding in the confines of the calf troughs. This is supported by the finding that samples of birds caught in a dairy unit on the same farm, where less nutritious food was presented in long, open troughs and where there was much spillage, contained over 50% females. The calf unit troughs, in which barley and high-protein concentrates are available, represent a highly competitive feeding situation for Starlings, and Feare & Inglis (in press) found that in these situations males tended to have a competitive advantage over females. Intra-specific competition for feeding space at the calf feeding troughs may explain the difference in the distributions of female Starlings in the 1975–6 and 1976–7 winters (Table 2). In the latter winter both the number of Starlings on the farm and the size of flocks feeding at the calf unit were higher than in 1975–6 (Table 1), suggesting that competition for feeding space would have been more severe in 1976–7. As males can feed more efficiently under these competitive conditions, the presumed presence of a higher total number of males in the local population in 1976–7 may have forced more females to feed away from the calf unit, e.g. in the dairy or in grass fields close to the farm.

Even in 1977–8, when human disturbance prevented flock size in the calf unit reaching the levels attained in the previous two winters, there was a tendency for sightings of birds tagged there to be concentrated close to the farm. This fidelity of birds to a feeding area selected early during the winter (Fig. 1), demonstrated particularly by those individuals for which there was a large sample of sightings (Fig. 2), has important implications with

respect to the Starling's potential to transmit disease. The results of this marking study suggest that Starlings are unlikely to transmit disease directly by travelling, during a feeding day, from farm to farm (e.g. see MURTON, 1964), from human waste disposal areas to farms, or from either of these areas to garden bird tables or other places where people are likely to come into close contact with Starlings.

However, direct transmission remains a possibility owing to the communal roosting behaviour of Starlings. When Starlings left the study farm in the afternoon they congregated in pre-roost assemblies with flocks of Starlings from many other feeding areas, including birds that had fed at other farms, at the sewage treatment plants and within the City of Winchester (and sometimes birds from the larger town of Southampton). Some of the pre-roost assemblies were in trees or bushes, where the birds rested or preened, while other assemblies involved intense feeding in cereal stubble or grass fields (and at a farm outside this study area in a pig feeding unit). In the latter situation the transmission of pathogens directly from a daytime feeding area to a farm on which the birds assemble, and also indirectly between birds from different daytime feeding areas, may be possible. A more remote possibility is that birds that pick up a specific pathogen one winter may carry this pathogen until the following winter, since SPAANS (1977) has shown that wintering Starlings frequently do not return to the same wintering area each year.

Nevertheless, subordinate birds in the farm population studied here, which may never attempt to feed in the calf unit and which have not, therefore, been wing-tagged during this study, may be more mobile in terms of their local movements. This possibility remains to be investigated.

Summary

A study of local movements of Starlings using wing-tagged birds showed that individuals were faithful to the feeding areas they selected at the beginning of the winter, with few birds feeding more than 400 m from the calf rearing unit where they were originally caught and marked. Male Starlings predominated at this calf unit, probably due to competitive advantage over females, and in a year when the number of Starlings feeding at the farm was high females fed further from the calf unit than when numbers were smaller. The Starlings' fidelity to feeding areas suggested that direct transmission of disease between feeding areas was unlikely, except when the birds travelled from their daytime feeding areas to pre-roost assemblies in the evening.

Acknowledgements

I am grateful to Messrs P. J. JONES, and E. J. MUNDY, successive Directors of Bridgets Experimental Husbandry Farm, and Mr. C. H. RISK, Area Manager responsible for Winchester sewage treatment plants, for permission to use their facilities, and to Messrs P. W. DAVIS, R. ROBERTSON and P. A. SCOLARI for assistance with the field observations. Mr. E. N. WRIGHT made helpful improvements to a draft of this paper.

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GRUPPENGESPRÄCHE

SPECIAL INTEREST GROUPS

Die folgenden Kurzfassungen sind unverändert aus der auf dem Kongreß vorgelegten Broschüre übernommen.

An der Stelle des Autors steht hier jeweils der einladende Organisator. Auf die Angabe des Veranstaltungsdatums wurde verzichtet.

Avian Functional Morphology

Walter J. Bock

Many diverse approaches to functional morphologies are used; these range from direct observations based on motion analyses, EMG and other experimental techniques to theoretical analyses based on a knowledge of physiology and to comparative studies. Discussion will focus on actual investigations and on the technical details of the methods employed.

Department of Biological Sciences, Columbia University, New York, N. Y. 10027, U.S.A.

Endocrinology of Reproduction and Neuroendocrinology

Brian Follet

Abstract not received.

University College of North Wales, Department of Zoology, The Brambell Laboratories, Bangor Gwynedd LL57 2UW, United Kingdom

Mechanisms of Temperature Regulation in Birds

Werner Rautenberg

Besides current problems in temperature regulation two subjects should be discussed preferably. 1) The interaction of temperature signals in the regulation of body temperature in birds. Characteristics and localisation of cutaneous and central temperature-sensitive structures, stimulus-response analyses showing receptive areas for triggering effector mechanisms and models of the regulatory mechanism. 2) The set-point adjustment in temperature regulation during circadian rhythms and exercise.

Ruhr-Universität Bochum, Tierphysiologie, Postfach 10 21 48, D-4630 Bochum

Circulation and Respiration—Suggestions for Research Development

H.-R. Duncker and K. Johansen

In continuation of the discussion from the symposium on circulation and respiration the deficit in our present knowledge should be emphasized to demonstrate some possibilities in which the further research in this field should develop. Reference should be made to thermoregulation, metabolism, flight energetics and breeding and how these factors influence circulation and respiration and have led to different specialisation.

Zentrum für Anatomie und Cytobiologie, am Klinikum der Justus Liebig-Universität, Aulweg 123, D-6300 Gießen

Investigation of Bird Flight—An Interdisciplinary Challenge

H. Oehme

Attempts should be made to find ways of interdisciplinary co-operation by means of which the mainly biophysically oriented problems of bird flight can be approached and solved. Information from ornithologists, functional-morphologists, zoophysiologists, aerodynamicists and technical physicists must be coordinated in order to solve these problems.

Zoologische Forschungsstelle im Berliner Tierpark, Deutsche Akademie der Wissenschaften zu Berlin, Am Tierpark 41, DDR-1136 Berlin-Friedrichsfelde

On the Definition of the Term Navigation

K. Schmidt-Koenig

Several attempts have been made in the past to define navigation. Recent findings question at least some of the propositions of the prevailing definitions of the term navigation, thus requiring attempts for a new definition.

Universität Tübingen, Institut für Biologie III, Beim Kupferhammer 8, D-7400 Tübingen 1

Integration of Auditory Physiology, of Control of Vocalization and of Bioacoustic Ecology

Johann Schwartzkopff

By the round table session, the opportunity of discussing questions of common interest is offered. The participants of the symposia may discuss auditory communication in the broadest sense, and also other ornithologists who are concerned with these areas. The problem of interdisciplinary areas between morphology, physiology, ecology, and ethology, as related to hearing and vocalization, are to be dealt with especially. Thus some of the existing gaps in our current understanding could be localized and perhaps bridged. However, it is not intended to repeat the presentation of the respective symposia. A direction in the discussions towards the most urgent future research work in the field is hoped for.

Lehrstuhl für Allgemeine Zoologie der Ruhr-Universität Bochum, Postfach 10 21 48, D-4630 Bochum

International Co-Operation in the Collection, Preservation and Exchange of Bird Sound Recordings

Jeffery Boswall

The need for international co-operation in the setting up and operating of libraries of avian sound registered particularly on tape and commercial gramophone records;

the need for standardized storage methods, "labelling", cataloguing, technology and use facilities; the problems of "copyright"; the promotion of international exchange of first generation copies; and the dissemination of facts about the existence of libraries.

Birdswell, Wraxall, Nailsea 3418, GB Bristol, BS19 1JZ, United Kingdom

Social Behaviour

Russell P. Balda

The goal of this discussion group is to a) review the present state of knowledge on altruism in birds, b) present new important findings where possible, c) explore the strengths and weaknesses of present theories, d) indicate areas of future research.

Universität Bielefeld, Fakultät für Biologie, Postfach 8640, D-4800 Bielefeld

Raptor Conservation—The Need for an International Approach

Joseph R. Murphy and Clayton M. White

The intent of this discussion group is to provide a forum for exchange of information dealing with field studies and management proposals relating to raptors, with special emphasis on neotropical species. Attention will be given to means by which resource management agencies of the various governments can become involved to a greater extent in raptor conservation.

Brigham Young University, Department of Zoology, 167 WIDB, Provo, Utah 84602, U.S.A.

Probleme der Angewandten Ornithologie

Herbert Bruns

Diskussion über aktuelle Probleme der Angewandten Ornithologie, insbesondere über die folgenden Themen:

Vögel und Schadinsekten, Vögel und Kulturpflanzen, Vögel und Pestizide, Abwehr und Verhütung von Vogelschäden in Land- und Forstwirtschaft, Hygiene, Flugverkehr u. a.

Internationale Union für Angewandte Ornithologie, Weiherallee 29, D-6229 Schlangenbad 5

Ökologie der Sylviinen
Ecology of Old World Warblers (Sylviinae)

Hartmut Walter

In zunehmendem Maße benutzten Einzelpersonen und Institute die artenreiche Unterfamilie der Sylviinen als Modellgruppe für ihre Untersuchungen. Augenblicklich

werden Einnischungen von Gattungen und Sylviinen-Gemeinschaften, Mechanismen der Koexistenz und zwischenartliches Verhalten, Mechanismen der Habitatwahl, Populationsdynamik, Ökomorphologie, Lautäußerungen, jahresperiodische Prozesse und Orientierung dieser Vogelgruppe bzw. anhand dieser Vogelgruppe untersucht.

Das Gruppengespräch soll die Teilnehmer über laufende und geplante Untersuchungen an Sylviinen informieren und die Arbeiten koordinieren und evtl. auch neue Schwerpunkte setzen.

University of California, Department of Geography, Los Angeles, CA 90024, U.S.A.

Bird Nesting and Predation, a Temperate-Tropical Comparison

Yoshika O. Willis

Nest predation is often high in tropical regions, but Amazonian studies suggest moderate rates. High rates occur for marshes and for concentrations of nests in non-tropical areas. Theories of low clutch size and dispersion effects in the tropics need reevaluation. Tropical-temperate comparisons must become more precise statistically.

Universidade Estadual de Campinas, Avenida Modesto Fernandes s/no., Barao Geraldo, 13.100 Campinas, S. P. Brazil

Affinities and Classification of the Passeriforme Birds

Walter J. Bock

The Passeriformes have always presented problems on all levels for avian taxonomists starting with their relationships to other orders, subdivision into suborders, delineation of families and ending with the affinities of individual problem genera. Classification and phylogenetic relationships of diverse passeriforme groups will be discussed.

Department of Biological Sciences, Columbia University, New York, N. Y. 10027, U.S.A.

Phylogeny of Old World Ratites

E. G. Franz Sauer

Discussions are based on reports by invited participants and on podium calls. Emphasis is placed on the questions of origin, adaptive radiation, morphogenesis, biochemical aspects, and relationships of ratites. Morphology includes bones and eggshells. Faunal characteristics are tracked through biostratigraphic evidence. Attempts are made to circumscribe the distribution during the Miocene and Pliocene, to trace routes and causes of range expansions and subsequent disappearances, and to establish a systematic pattern for further research.

Zoologisches Institut und Museum Alexander Koenig, Adenauerallee 150—164, D-5300 Bonn 1

Avian Speciation and Zoogeography in South America

Lester L. Short

Abstract not received.

Curator, AMNH, and Adjunct Professor of Biology, Graduate Faculty, City University of New York, New York, U.S.A.

Historical Bird Collections in Museums

Peter Morgan

The aim of this special interest group is to bring together ornithologists working with or interested in collections containing important type, extinct or geographical material. Many collections collected during the nineteenth century, now housed in Europe and elsewhere, contain specimens of interest to workers world wide and the discussion will hopefully increase communication and coordination concerning the existence of these collections. Curators especially are asked to bring details of collections, especially non published material, concerning collectors represented in their collections.

Keeper of Vertebrate Zoology, Merseyside County Museum, William Brown Street, GB Liverpool L 3 8EN

Problems in Breeding and Keeping the Congo-Peacock *Afropavo congensis* Chapin

R. Van Bocxstaele

Since 1959, Antwerp Zoo has been working on a breeding program for Congo-peacocks. No specimens have been exported from Zaire since 1962.

There are still unsolved problems: a growing birthsurplus of females; percentage of fertilisation declining; large percentage of death among chicken; adult birds: atheromatosis and aneurism—diet problem?

Koninklijke Maatschappij voor Dierkunde van Antwerpen, Koningin Astridplein 26, B-2000 Antwerpen, Belgium

Development of a Numbering System to Identify all Species of Birds

James R. Karr

The increasing use of computers to store and process data about birds has precipitated a number of problems. One such problem is that of identifying the species (or higher taxonomic unit) under consideration. Many local ornithological organizations

have solved this problem by identifying each species in their area with a unique code number (AOU number, for example). However, ornithologists increasingly have a wider geographic perspective, making the old system of identifying species difficult or impossible to use. The purpose of this discussion is to examine the need for a uniform, world-wide coding system for identifying all species of birds. In addition, we will discuss several systems that have been used in the past and try to develop a workable system that can be recommended to the IOC.

Department of Ecology, Ethology and Evolution, Vivarium Building, University of Illinois, Champaign, Illinois 61820, U.S.A.

TAFELVORTRÄGE

POSTER PRESENTATIONS

Die Kurzfassungen der Tafelvorträge sind alphabetisch nach Autoren-Namen geordnet, die Nachträge ohne Kurzfassungen auf Seite 1414 angefügt.

Dies ist ein unveränderter Nachdruck der auf dem Kongreß vorgelegten Broschüre.

Sex hormones and vocalization in domestic pigeons

Michael Abs

During juvenile development the vocal system of the domestic pigeon *(Columba livia domestica)* is influenced by hormones of the hypothalamic—pituitary—gonadal axis. The gonadotropin content of the pituitary estimated by gel-electrophoretic separation indicates a rise during development. Plasma luteinizing hormone levels were measured in 61 birds and an increase of about 100% was found (Abs, Ashton & Follett 1977). The surface of the nuclei of the interstitial cells of the testis (14 birds) increased by about 20%. Measurements of androgen levels in the plasma are under investigation. All these changes occur when the pigeons are 7—8 weeks old, fully grown, but not yer mature. At this time they pass the breaking of the voice, i.e. a sudden change of vocalization frequencies from about 3.0 kHz to 0.3 kHz. This change is accompanied by an increase in the weight of the vocal apparatus and of one of the expiratory muscles (M. obliquus externus abdominis). The time of the breaking of the voice can be advanced by application of androgens, delayed by castration or inhibited by hypophysectomy. From these data a model of the hormonal influences on the vocalization system is derived and discussed.

Ruhr-Universität, Lehrstuhl für Allgemeine Zoologie, Bochum, Germany.

Influence of Anthropogenic Factor upon Avifauna

Main Ways of Conservation of Rare and Endangered Species

I. A. Abdusaljamov

Man's influence on avifaunas becomes greater every year. Middle Asia is a good example.

As a result of intensive activity of Man over the last 50—60 years, a small agrarian economy of this region has become an intricate industrial complex with highly developed agriculture and culture.

Deserts, semi-deserts have been artificially irrigated, developed and cultivated for cotton and other agricultural products. Marshes have been drained and riparian forest areas reduced. Cotton plantations, orchards, towns, villages, plants, highways and irrigation channels have been built. These changes have influenced avifauna of the Middle Asia.

The area and number of *Otis tarda, Otis undulata, Burhinus oedicnemus, Pterocles orientalis* was noticeably reduced. In typical nest and wintering places these species are rare.

The anthropogenic factors have caused the reduction of the nesting area and numbers of *Ciconia ciconia* and of three subspecies of *Phasianus colchicus. Eulabeia indica* has become rare in the Tien Shan and the Pamirs.

Man's interference has been favorable for the extension of some species. Urbanization in Middle Asia caused a sharp expansion of *Streptopelia senegalensis, Hirundo rustica, Hirundo daurica, Acridotheres tristis* and *Passer montanus.*

A wide range of works is organized here for the protection and recovery of rare and endangered species. A comprehensive network of Wildlife Refuges and Protected Areas were established for protection and recovery, as well as reacclimatization of species.

Institute of Zoology and Parasitology of the Academy of Sciences of the Tadzhik Soviet Socialist Republic, Dushunbe, the U.S.S.R.

Specific Distinctiveness in the Vocal Repertoires of North America Crossbills *(Loxia)*

Curtis S. Adkisson

Distinctiveness in bird song among sympatric, related species is an established principle. Among the cardueline finches specific distinctiveness in certain flight calls has been shown also, but congenors apparently show great similarity in alarm and some social vocalizations. In the sympatric populations of the North American crossbills, *Loxia curvirostra* and *L. leucoptera,* vocal distinctiveness is more pronounced than in other sets of congeneric finches. Even flying-predator alarm calls, shown to be similar in some unrelated birds, are greatly different. The vocalizations of these crossbills differ not only in the structure of individual notes, but also in the timing of delivery. Such differences in timing are especially pronounced in flight calls.

There is very little evidence of hybridization between *L. curvirostra* and *L. leucoptera.* Hybrids have been produced in captivity, however, and no such obviously hybrid specimens have been found in museum collections. In North America, at least, barriers against interbreeding are quite effective. In these nomadic birds, social vocalizations involving flocking, rather than primary songs of the sort typical of most passerines, could inhibit hybridization. It is proposed that crossbills use flight calls to identify potential flockmates at a distance, and individuals choose a sexual partner primarily from among these flockmates. The former hypothesis is supported by field experiments which show that crossbills approach playback of conspecific flight calls, and not that of heterospecific calls. The latter hypothesis will be tested in future experiments with captive birds.

Virginia Polytechnic Institute and State University Blacksburg, Virginia, USA.

Historical Notes on the Bird Collection of the Genoa Museum of Natural History „G. Doria"

Gianna Arbocco*), Lilia Capocaccia*) and Carlo Violani**)

The Genoa Natural History Museum "G. Doria" can boast of a particularly rich ornithological Collection of remarkable scientific value, due to the presence of an outstanding number of type specimens as well as rare and extinct forms.

The Collection originated and was increased thanks mostly to the exploring and collecting expeditions at the end of last century and at the beginning of the present one.

Valuable collections were brought back by Beccari, D'Albertis, Loria and Modigliani from Australia, New Guinea and Indonesia; by Fea from Burma and Western Africa; by Bottego, Antinori, Citerni, Ragazzi, Ruspoli, Franchetti and Patrizi from Eastern Africa; as well as by Bove and Vinciguerra from South America.

Such an impressive Collection has been the object of study by many distinguished Ornithologists, outstanding among these being Tomaso Salvadori, who wrote well over 80 memoirs devoted to the material preserved in the Genoa Museum, describing over 250 species new to science in addition to a good number of new genera.

Among the best represented series of birds, must be mentioned those of the Paradisaeidae, Psittacidae, Alcedinidae, Casuariidae; among the extinct species should be remembered: *Fregilupus varius, Lampribis rothschildi, Moho nobilis, Ectopistes migratorius* and the last Italian *Francolinus francolinus,* shot in Sicily in 1869.

*) Museo Civico di Storia Naturale "G. Doria", Genova (Italia).
**) Istituto di Ecologia Animale ed Etologia, Università, Pavia (Italia).

Short- and long-term effects of testosterone on the social behaviour of male ducks

J. Balthazart

We have already demonstrated that testosterone propionate injections will readily elicit an intense sexual behaviour in ducklings as well as in immature male ducks. On the contrary, the hormonal treatment had very few effects if any on social display: it stimulated this behaviour only in one out of seven experiments. These results correlate well with the known variations of the plasma levels of hormones and of behaviour during the reproductive cycle: the variation of plasma testosterone is correlated with that of sexual behaviour but not social display. Besides its rapid effects, the repeated injection of testosterone propionate induces long-term changes in the behaviour. During several independent experiments, we observed after the termination of testosterone injections, a strong inhibition of sexual behaviour and of social display. This inhibition lasted up to four months.

Plasma FSH, LH and testosterone were repeatedly assayed in these animals in an attempt to correlate the behavioural inhibition to modifications in the hypophyso-gonadal activity.

The circulating levels of these hormones were not systematically changed in the birds which had been injected with testosterone though a slight decrease in plasma testosterone was observed once. Other possible hormonal bases for the behavioural inhibition will be briefly discussed.

Laboratoire de Biochimie générale et comparée, 17 place Delcour, B-4020 Liège, Belgium.

Nomina Anatomica Avium)*
An annotated Anatomical Nomenclature of Birds

Julian J. Baumel**)

Nomina Anatomica Avium is the publication of the ICAAN project, underway for the past seven years. ICAAN (International Committee on Avian Anatomical Nomenclature) consists of 80 scientists world-wide who collaborated in compiling and codifying the anatomical names (and annotations) applicable to Class Aves generally. Similar nomenclatures already exist for man and veterinary mammals.

Diversity of terminology renders the present literature of avian anatomy ambiguous and confusing. Physiological, biochemical, taxonomic, behavioral, paleontological, and pathological investigations all require an anatomical basis, and in preparing uniform avian anatomical names the requirements of the various groups of scientists concerned with avian anatomy were considered.

An internationally acceptable anatomical nomenclature will enhance communication among avian scientists of different language groups, save research time and effort, and facilitate storage and retrieval of information by computers and from the various literature abstracts and indexes.

For greatest benefit *Nomina Anatomica Avium* should be put into general use without delay. Editors are urged to insist that the official Latin form of the anatomical terms be used in titles of articles and books, in key-words supplied for data-retrieval systems, and on the occasion of the term's first appearance in the text (the treatment now applied to scientific names of species and other taxa). All avian scientists should utilize the *Nomina* in their publications and require its use in theses and dissertations of their graduate students.

*) Book in press (Academic Press, London), publication date fall of 1978. Supported in part by the U.S. National Institutes of Health (NIH grant LM 02420 from the National Library of Medicine).

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The influence of learning on simple and complex songs of Marsh Tits *(Parus palustris)*

Peter H. Becker

Marsh Tits are singing simple song types consisting of series of one note ("Klapperstrophe") and complex song types, which combine different notes to repeated groups. Nestlings were isolated in sound proof chambers and reared up in 4 experimental groups. Group I heard natural songs from a tape, group IV artificial songs.

In all groups the characteristic "Klapperstrophe" develops. Its pattern is innate probably, its details (group- or population-specific) have to be learned. The variability of the "Klapperelement" in the groups is similar to the variability of this note in song of wild

Marsh Tit populations. The complex song types, however, cannot be found in anyone of the groups; they are transmitted by learning (tradition). The isolated birds instead develop improvised songs. Group members share most of their songs. Females can sing too. Group IV learned one artificial song, but group I none of the played natural songs.

Already in fall the young Marsh Tits are singing. Nearly all songs of their later repertoire are crystallized.

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Wintering Smew in the Netherlands

A. J. Beintema

In recent years the Smew *(Mergus albellus)* has been wintering in the Netherlands in numbers hitherto unknown in Western Europe (up to 21,000 in 1977). It is not known where these birds stay in spring and autumn. The high percentage of adult males (40 %) suggests that most juveniles do not winter in Holland. Other mass concentrations are known from the sea of Azov and the Volga delta. The recovery of a Dutch ring from 76° E suggests a great importance of Dutch waters. Most Smew stay in the IJsselmeer, where groups of over 2,000 individuals can be seen. When diving for fish there is a high degree of synchronisation: over 97 % of the birds may be below the surface simultaneously. This social feeding is rarely seen in small groups. Another phenomenon, which is only known from the mass occurrence in the IJsselmeer, is a segregation of feeding and sleeping grounds. From sleeping grounds around the southern IJsselmeer the birds migrate daily to and from the lake, in mass flights. They sleep on the water, separated from the main lake by a dyke only. The significance of the Dutch winter population has not yet been recognised in international literature.

Research Institute for Nature Management Leersum, Netherlands.

Some possible determinants of full song in *Sylvia* warblers: A comparative approach

Hans-Heiner Bergmann

The warbler genus *Sylvia,* consisting of about a dozen European species, provides an excellent subject for comparative studies. This paper aims at discovering some correlations between full song characteristics and morphological as well as ecological data.

The species differ with regard to all these. Their body weights range from 9 grams to more than 20 grams. There are at least two characteristics of full song showing high correlations with the body weight of the species concerned: the mean pitch of clear tone elements, and the mean element rate (tempo) of the songs.

Sylvia warblers are predominantly inhabitants of the bush vegetational layer. The density of tree and bush layers in the breeding habitats are fairly constant for each species but highly variable between species. The songs consist of clear tones and short noisy elements in differing combinations, these being species-typical. There is a significant negative and non-linear correlation between the density of the tree layer in the breeding habitats and the percentage of short wide-range elements in the full song. This finding is interpreted as an effect of adaptation to the acoustical properties of tree stands of differing density. While some song characteristics seem to be determined by constituational data such as body dimension, others appear to be adaptive with regard to the species-specific ecology.

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Bill tip organ and its primary projections in the brainstem of the mallard *(Anas platyrhynchos L.)*

H. Berkhoudt

Mallards discriminate hard edible peas from softer inedible fake-peas (Zweers et al., 1977). Tactile and gustatory afferents in the bill tip could be responsible for this ability. The occurrence of taste buds far rostrally in the beak has been demonstrated by Berkhoudt (1977). Mallards show a highly organized tactile system in the very bill tip (Berkhoudt, 1976), comparable to the "bill tip organ" of geese (Gottschaldt & Lausmann, 1974). The very hard horn of the maxillary nail comprises 40 dermal papillae of about 1 mm length. In the mandibular nail 190 similar papillae are orientated at right angles to those of the maxillary nail. Proportional to the diameter of the papillae, 6—18 Grandry corpuscles distally and 6—14 Herbst corpuscles proximally are stacked around a central core of afferents. The orientation of both types of mechanoreceptors adapts them functionally to lengthwise compressions of the papillae. The projections on the brainstem of the trigeminal nerve innervating the bill tip organ, which were established neuroanatomically by Dubbeldam (1977), is studied by electrical stimulation of these branches and stereotactic (Zweers, 1971) recording in the main sensory nucleus of the Vth nerve. This gross picture is differentiated by mechanical stimulation of the different parts of the nail and simultaneous recording in the brainstem.

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Co-operative breeding in ostriches

Brian Bertram

In East Africa, ostriches nest communally. A male establishes a territory, and several females lay in a nest within it. Only one of the females, the 'major' hen, takes turns with the male in all the work of guarding the nest and subsequently in incubating the eggs. Guarding is very necessary, because there is a high rate of predation on the eggs, by Egyptian vultures, jackals and hyaenas. In many nests, more eggs are laid than can be covered by an incubating bird. Therefore, before incubation starts a number of eggs are pushed to an outer ring where they are not incubated. There are some indications that the major hen's own eggs are unlikely to be among these doomed outer eggs. A pair of ostriches which has hatched chicks apparently competes with other similarly successful pairs for guardianship of all the young; thus very large mixed broods may be formed.

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Energetics of Incubation in Starlings *(Sturnus vulgaris)*

Herbert Biebach

The energy requirement of eggs during incubation can be calculated from the difference in energy consumption of an incubating bird on a nest with and without eggs. Direct metabolic measurements of incubating and non-incubating starlings as well as estimations of nest insulation lead to a calculation of the eggs energy requirements: 0.41 · BMR to 0.08 · BMR at 20 °C and 1.23 · BMR to 0.57 · BMR at −10 °C ambient temperature (Ta).

The incubating bird is the source of this energy. A comparison of the energy consumption in individual birds during and outside incubation showed that there was no extra cost for incubation in the thermoneutral zone and, up to 35 % more at −10 °C Ta. In a second experiment where an artifical clutch of copper eggs was heated or cooled and the metabolic reaction of the incubating bird could be followed, there was also no extra cost of incubation in the thermoneutral zone.

By cooling the copper eggs, the heatflow from the broodpatch could be increased up to two times the value necessary to keep the eggs at 37 °C when Ta is −10 °C. It is concluded that the capacity for heat transfer from the broodpatch as well as the total heat producing capacity of the bird are probably not responsible for desertion of clutches under natural conditions when Ta is low.

The control of population size in spruce grouse

D. A. Boag, D. M. Keppie, K. H. McCourt, P. W. Herzog, J. H. Alway

Gain and loss of individuals in a population of spruce grouse *(Canachites canadensis)* was studied in southwestern Alberta from 1965 to 1975. Recruitment in spring (gain) was confined to grouse less than a year old; most (74 %) were immigrants, females exceeding

males by 1.64:1. Grouse in all age groups suffered loss. Among adults loss was through death, most (64%) occurring between April and August. Among juveniles, loss was through death, mainly between the egg stage and independence (79%), and dispersal. Of juveniles surviving, 72% emigrated in autumn or the next spring, females exceeding males by 1.24:1. Survival of juveniles to independence, as a proportion of the potential number, varied inversely with size of the spring population. Emigration, apparently spontaneous in autumn, seemed to be stimulated in spring by aggressive behaviour of resident territorial birds and thus could be influenced by spring population density. However, at the densities encountered (8.4 to 20.6 grouse/100 ha), the main factor controlling the size of spring populations was the relative reproductive success the previous summer, a density-dependent parameter reflecting levels of predation.

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Breeding density of the european starling — *Sturnus v. vulgaris L.*

A. F. de Bont

It is generally accepted that the european starling—*Sturnus v. vulgaris L.*—has shown the latests decades a marked increase in numbers and also an extension of his breeding area.

Although several factors are certainly involved they can evidently be brought back to better breeding success and (or) less mortality. What is true for the whole of the europeen starling population is not neccessarely so for the population of a given area. Kind of nest-places, density of nests and also density of wintering flocks were studies in southern Limburg (Belgium).

Results are exposed and discussed.

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Systematic Relationships among the Anatidae: a comparative serological study

Peter Diedrich Bottjer

Systematic relationships among the Anatidae were studied using comparative serology. Antisera against whole plasma were made for eight species representing each of eight polytypic tribes. Blood samples from seventy species were used in making cross-comparisons by immunoelectrophoresis and haemagglutination inhibition.

The intents of the study were 1) to test for monophyly of the various tribes, 2) to place certain aberrants in their proper tribe, and 3) to determine intertribal relationships, thus producing a probable tribal phylogeny for the family. Sample results are presented in

all three categories. The large polytypic tribes were found to be natural groups with the possible exception of the Cairinini. *Anseranas* was very distant from all other waterfowl. Summary statements are given for *Cereopsis, Coscoroba, Lophonetta, Somateria,* and others. A probable tribal phylogeny is presented along with a classification. Major changes occur with respect to the stifftails (Oxyurini) and the sea ducks (Mergini).

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Regional Survey on Nesting colonies of *Ploceus Cucullatus*

M. da Camara-Smeets

From August to October 1975, 31 nesting coloniès of *Ploceus cucullatus* have been identified within on area of 3,000 km² South of Lake Chad (Africa) between 11° and 13° of latitude Norths.

The number of nests and the productivity of each colony have been estimated by means of several samplings, during the course of the nesting season. The general pattern of the nesting colonies have been determined.

The differences between bush colonies and village colonies are not relevant. The average length of nesting season is 70 days. In each colony the number of nests increases during first month and then decreases. The average number of fledgling attemps is 4 for each colony, with a period of about ten days from one to another. At regional level, reproductive periods and fledgling attemps are well synchronised. Each nest carries in average 2,4 eggs and 1,9 youngs, the reduction taking place in one time at hatching.

Due to the regional synchronism the period of most intense reproduction activity at which the number of nests reach its maximum, can be determined. An interesting relation with a prediction value seems to exist between the number of nests at the peak of the reproduction and the total number of fledglings.

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Seasonal Variation in Daily Food Consumption and Daily Feeding Rhythm in Relation to the Body Weight Cycle of Subtropical Spotted Munia

Asha Chandola and Sushama Pavgi

The body weight of nonmigratory spotted munia exhibits a distinct annual cyclicity. In an attempt to work out the environmental correlates of this cycle investigations have been made on the total food consumption and daily feeding rhythm over 18 months.

Five adult males were established individually in ambient conditions of temperature and photoperiod (food and water ad libitum). Observations on hourly and daily food con-

sumption were made almost every month. A significant seasonal variation in daily food intake is revealed. From the results it can be concluded that the annual gain in body weight of spotted munia is not due to an increased caloric intake. Results also indicate that there is a seasonal change in daily feeding pattern. Feeding occurs in one or two prominent peak periods except in autumn when it is almost continuous. In this context, it may be mentioned that artificially induced (prolactin injections) gain in weight is accompanied by an abolition of the rhythmic pattern of feeding in spotted munia (Chandola, A. & Pavgi, S., 1978, Gen. comp. Endocrinol., in press). How far, if at all, the change in daily feeding pattern could contribute to the concomitant seasonal gain in body weight of this bird remains to be explored.

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The Annual Cycle of the Red Bishop *Euplectes orix*

Adrian Craig

The biology of the Red Bishop was studied over a three year period in Natal, South Africa. The breeding season of this polygynous ploceid coincides with the summer rainy season, and the amount of breeding activity appears to be correlated with the amount of rain during the previous year. Breeding success at the colony studied was low; predation was the major cause of nest failure.

This species is sexually dimorphic, the males being larger than the females. The population sex ratio was significantly biased in favour of males, but there was an excess of females in the breeding population, since males do not breed until their second year. Adult males undergo a partial moult at the start of the breeding season and acquire a distinctive nuptial plumage. This is shed again at the post-nuptial moult, and in eclipse plumage they resemble the females. The entire population, including the juveniles, undergoes a complete moult at the end of the breeding season. The birds' weight varies seasonally, with peaks early in the breeding season and again during the moult. The lowest annual weights are recorded during the dry season, and the flocks may make local movements during this time.

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Biogeography of Afrotropical Passerine Birds

T. M. Crowe

The distributions of 1 099 Afrotropical (= Ethiopian) passerine taxa are analyzed by computer to determine possible zoogeographic zones and patterns of species richness. Six subregions, nine provinces and 15 districts are recognized. The boundaries of these zones accord well with these suggested by other authors who have used a more subjective,

non-quantitative methodology. Species richness is highest at the equator. At least three equatorial forest areas of relatively high species richness correspond well with disjunctly similar districts. This result suggests that these areas may have served as „refugia" during the Pleistocene epoch.

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The Principles of Leaping Flight—a Computer Simulation

Michael J. Csicsáky

During the body-gliding interval, small birds adapt a projectile contour. Therefore, it appeared appropriate to develop a mathematical model for the body-gliding trajectory based on ballistic equations. These calculations should emenate from reliable parameters in order that they produce biologically significant results. For this reason the application of ballistic equations was preceeded by experimental studies in a wind tunnel:

— in living zebra finches *(Taeniopygia guttata)*, body drag was measured with respect to different inflow velocities
— in plaster models, body lift was measured with respect to different angles of attack

Starting from the experimental findings trajectory calculations were carried out and, amongst others, the following predictions were stated:

— maximum range and minimum sinking speed are obtained by an initial angle of 45° and by use of body-lift during the descending phase of the gliding parabola
— maximum gliding speed is obtained by flat initial angles and by renunciation to body-lift generation
— high velocity flight and highly undulated trajectories are mutually exclusive

These and further predictions are being checked against free flight trajectories of zebra finches filmed in a wind tunnel. A description of methods and results are the object of this poster presentation.

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Fitness to Wildlife of some breeding-born specimens of the Barbary Partridge *(Alectoris barbara* Bonnaterre)

Attilio Mocci Demartis

Examining the causes for the regression of the Barbary Partridge in Sardinia, he analize individually the various determining factors that could influence either positively or negatively a release of some specimens with the purpose of repopulation.

Afterwards he reports on the data of eight experimental releases, done with a total of 97 bred and 3 captured individuals, between November 1975 and March 1976.

Following that, he ascertained the certain death of six specimens, and the disappearance of all the others from the place in which they were released, he advances some hypotheses on the probable causes that could have negatively influenced these releases, backed up by the previous analogous experiences made in other places on the Barbary Partridge or on other species of the gen. *Alectoris* by various authors.

Finally he givens some useful advice to avoid in the future, wherever possible, in the useless waste of specimens and money.

c/o Istituto di Zoologia, Viale Poetto No. 1, 09100 Cagliari, Italia.

Role of Rostral Brainstem in Salt Gland Control of Conscious Pekin Duck

Hans Deutsch and Eckhart Simon

The rostral brainstem of birds regulates water excretion of the kidney by controlling ADH production and release. Its involvement in the control of salt gland function has, however, only recently been demonstrated: Cooling the rostral brainstem of Adelie penguins and Pekin ducks inhibits salt gland secretion. These observations confirm that temperature dependent brainstem neurons take part in the control of this osmoregulatory effector organ, but they do not indicate whether these are receptive, integrative or efferent neurons. During sustained stimulation of the salt glands by continuous intravenous infusion of 800 mosm. kg^{-1} NaCl, microinjections of hypertonic NaCl solutions into the rostral brainstem were performed. In control experiments, the same injections were made in animals, whose renal water excretion had been stimulated by intragastric infusion of tap water. While the microinjections caused antidiuretic reactions conforming to the hypothesis of brainstem osmoreceptors, the effects on salt gland secretion were equivocal. Thus, control of salt gland secretion by brainstem osmoreceptors cannot be considered as established. On the other hand, single unit recordings in the same brainstem region revealed neurons the activity of which could be influenced by changes of plasma osmolality.

Supported by DFG (Si 230/2)

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The Colour-Producing Structure in the Cryptic, Green Feathers of Fruit Doves *Ptilinopus*

Jan Dyck

The iridescent, metallic green plumage of some imperial pigeons *Ducula* spp. owe its colour to the presence, in the barbule cells, of layers of melanin granules. In the green plumage of fruit doves *Ptilinopus* spp. the colour is also due to melanin layers in barbule cells, yet the resulting colour is non-metallic, dull, completely different in appearance

from that of *Ducula*. Electronmicroscopy shows that the difference is due to a specialized shape of the *Ptilinopus* barbule cells.

The number of melanin layers varies between *Ptilinopus* species. From spectrophotometric measurements it is evident that the number of melanin layers is correlated with the purity of the reflected green light. The highest number of layers in the eight species investigated was found in *Pt.victor*. The structure found in *Pt. (Leucotreron) cincta* and *Pt.superbus* contains relatively few melanin layers and by this as well as other characters approaches the structure of the *Ducula* feathers.

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A Graphical Approach to the Avian Skull Biomechanics

Felix Ya. Dzerzhinsky

The functional abilities of any part of the skeletomuscular system depends on both its mechanical properties and the program of action as determined by the nervous system. A considerable amount of the mechanical properties of the mechanism proceeds from its configuration and macroscopical structure and therefore must be understood on the basis of its anatomy. Drawing of the simplified flat model of bird skulls are used for this purpose. The model includes the four-link mechanism of the upper jaw and mandible loaded by two muscle forces: by the dorsal adductors (the main force) and by the pterygoid muscle. The case of keeping prey motionless is considered. This is important from the biological point of view. It presents the state of equilibrium that is suitable for analysis in terms of statics as in this case all forces form an enclosed system. The flat model of jaw apparatus may be evaluated by this method first, in relation to the maintenance of the equilibrium and second on the ground of relative vector lengths which are indices of mechanical advantage.

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Sex Ratio in two Ploceids

C. C. H. Elliott

Studies were carried out on the Cape Weaver *Ploceus capensis*, a polygamous colonial species with marked size and plumage dimorphism, and on the Quelea *Quelea quelea*, a monogamous, but highly gregarious species with less marked dimorphism. In a total of about 3500 *P. capensis* sampled on many occasions a slight excess of males was found. In a total of 25,000 *Q. quelea* sampled over a wide area, a slight excess of males was also found. But in both species catches were made which were strongly biased in favour of one or other sex. These findings are examined in relation to the possible influences of segregation in flocks by age and sex, of the division of labour between the sexes, of size and plumage dimorphism and of the sampling technique. The results are compared with those from other weaver species and with those previously made on the Quelea. In the latter a gradual

increase in the proportion of males has been recorded, the male: female ratio reaching as high as 4:1 before returning to apparent equality at breeding.

Fao quelea project N'Djamena, Tchad.

Bird Communities and Spatial Patterns of Vegetation

Martin Erdelen

For the analysis of relations between birds and their environment, objective, quantitative, and statistically evaluable descriptions of vegetation seem highly desirable. To compare different vegetation measures, 22 study plots (mean area: 6.2 ha) were selected, including grassland, young afforestations, and older coniferous, deciduous, and mixed forests. Censuses of the breeding passerine birds were conducted by means of the mapping method. The structure of the vegetation was registered according to a modified version of the method proposed by Blondel et al. (Blondel, Ferry & Frochot (1973): Alauda **41,** 63—84; Blondel & Cuvillier (1977): Oikos **29,** 326—331): For 50 points along transect lines, the presence or absence of foliage was recorded at twelve different heights (0.25 to 32.00 m), within a field of view of 0.50 m diameter. Registrations at levels higher than 5.00 m were obtained by use of a telephoto lens. Additional observations with the „relascope", a simple and easily applicable optical device (Greig-Smith: Quantitative Plant Ecology, London 1964, p. 53; Gounot: Méthodes d'étude quantitative de la végétation, Paris 1969, p. 54), allowed the computation of the basal area (of trunks) per hectar for each tree species; from this the number of trees per hectar could be estimated by means of average tree diameters. Several vegetation diversity measures were computed, among which MacArthur's "foliage height diversity" and "plant species diversity" (e.g. Mac Arthur & MacArthur (1961): Ecology **42,** 594—598) as well as other information-theoretical indices suggested by Blondel et al. (loc. cit.). Relations between these indices were investigated, and their usefulness as predictors of bird community features (density, number of species, bird species diversity) was examined. Cluster analysis methods were used to group the study plots according to their vegetational structure and to their avifaunal composition, respectively.

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Behavioural differences associated with plumage dimorphism in *Zonotrichia albicollis*

J. Bruce Falls and D. J. Loncke

Two plumage types (white-striped and tan-striped morphs), differing in colour and intensity of head pattern and associated characters, have been described in the alternate (breeding) plumage of both sexes. Plumage is correlated with dimorphism in a large chromosome. White-striped birds tend to mate with tan-striped individuals (negative assortative mating). If a male or female is removed from its territory, it is usually

replaced by a member of the same morph. Although young of both morphs are produced in approximately equal numbers in both sexes, white-striped males and tan-striped females predominate among breeding adults. However, morph ratios vary among habitats within a geographic area.

White-striped males sing more often, both spontaneously and in response to playbacks, than do tan-striped males. Normally, only white-striped females sing. The incidence of song varies among these different members of the population as the breeding season progresses. Greater dominance of white-striped birds has been demonstrated during migration. However, territorial males of both morphs are equally likely to approach and attack models used in association with playback of song. An explanation based on behavioural differences between the morphs is proposed for the assortative mating.

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A long-term population study of Hobbies *Falco subbuteo* in Berlin

Dietrich Fiuczynski

There are some reports of decreasing breeding numbers of Hobbies in Germany whereas exact data are rarely known (cf. Blab et al. 1977 Red List, Thielke in World Conference Birds of Prey, Vienna 1975, Schroeder 1970 Ornith. Rundbrief Mecklenburg).

In Berlin 436 pairs of Hobbies were registered between 1956—1977 of which 377 were studied in detail. Although numbers were higher in the Fifties and early Sixties (maximum 1960: 31 pairs/146 km² forest area) the Hobby is still numerous (1977: 19 pairs, cf. Wendland 1953: 10—12 pairs/137 km² in similar habitat north of Berlin 1940—1951). Residue contents of 9 addled eggs range between 3.0 and 9.5 ppm (wet weight) DDE and 1.0 and 21.9 ppm PCB. The total load of chlorinated hydrocarbons obviously has no influence on reproduction as there is no correlation between the observed fluctuations in numbers and reproductive parameters such as brood size (2.41 fledged young/successful pair, n = 700 young, 290 pairs), breeding success (76.9 % of 377 examined pairs had fledged young) and reproduction figure (1.86 fledged young/examined pair) respectively.

Berlin, Germany.

Allopreening and Aggressive Behaviour in the Great Green Macaw (*Ara a. ambigua* Bechstein)

Gudrun Fritsche

The Great Green Macaw (Psittacidae) displays many conspicuous behavioural patterns that appear to be socially relevant. Two such patterns (allopreening and aggressiveness) were investigated in 2 captive groups. Birds readily formed pairs in both flocks.

Allopreening was well developed in that it was not restricted to the head, neck, and breast of the partner, as in most birds, but extended to most of the body of the partner. Allopreening birds often preened the same part of the body simultaneously.

An important component of aggressive behaviour was bill-fighting, a ritualized fight. The birds also had several threat postures that varied according to the level of aggression as indicated by different body and feather postures; e.g. bill-gaping was indicative of low levels and crouching of high levels of aggression.

In each group one pair dominated. In 2 years of observation subordinate pairs did not challenge the dominant pairs. Subordinate birds often performed bill-fights among themselves. The dominant pairs used only threats and other typical displays to maintain their positions. Bill-fights were used by the dominant pairs only when challenged by strange pairs.

There were no qualitative differences in allopreening and aggressive behaviour between the two sexes. The frequency of aggressive hehaviour, however, differed between males and females, as the former sex performed aggressive acts more frequently than the latter. These aggressive acts were most frequently directed toward other males.

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Bird pollination of the Crane Flower *Strelitzia nicholai*

Suzanne Frost & Peter G. H. Frost

The exploitation of *Strelitzia nicholai* (Musaceae) flowers by nectar feeding birds was studied in coastal forest in Natal, South Africa. *Strelitzia* flowers are specialized for bird pollination. The petals form a sheath enclosing the anthers. These open when the petals are depressed by an alighting bird. The stigma protrudes from the sheath and nectar accumulates in a cup at the base of the petals. Upto eight flowers occur in each horizontally-aligned bract. The flowers open sequentially and each lasts for three days. As the flower ages, the angle of the flower to the bract changes. Nectar production varies with age and is greatest on the second day (mean 140 $\mu l.hr^{-1}$) when the flower is between 10—25° from the horizontal. Nectar quality remains constant during the life of the flower at 10.8 ± 1.5 % sucrose equivalents, the energy value of which is 1.7 $j.\mu l^{-1}$.

Two forest sunbirds, *Nectarinia olivacea* and *N. veroxii*, made contact with the pollen on 24 % and 45 %, and with the stigma on 5 % and 6 % of their visits respectively. The birds fed preferentially at flowers aligned between 13—25° from the horizontal, indicating that flower angle was used as a visual signal to enhance foraging success. Competitive interactions were limited to displacement. *Strelitzia nicholai* flowers throughout the year, with a diminuition during the wet season. Thus the sunbirds are assured of a year-round food source, and the plants, a reliable and constant pollinator.

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Evolutionary and Geographical Radiation of Kingfishers

C. Hilary Fry

The kingfishers (Alcedinidae) comprise a monophyletic, cosmopolitan family of 90 species. The poster illustrates all of them, mapped in 22 groups, the species in each inferred to be of immediate common descent.

Of the living species the least derived (most primitive) are likely to be those (a) with simple feeding behaviour, swooping onto large arthropods and small vertebrates, (b) having relict or circumscribed ranges, and (c) being taxonomically isolated. By contrast the most derived (advanced) will be those with: specialised feeding (plunge-diving for fish, demanding anatomical adaptations); continuous wide ranges in seasonal habitats; and several close relatives. Using those criteria I find that nearly all primitive kingfishers are Malesian (s.e. Asia to s.w. Pacific), and infer that the family originated there, mainly as "insect"-ivores in Wallacean/New Guinean rainforest (that would be about the mid Tertiary, 20—25 million years ago).

The tree kingfishers (Daceloninae, c. 60 spp.) are generalised foragers, some in soil litter, others becoming predators, crab-eaters or fishers; they have invaded Africa, via Asia, on 4—5 separate occasions. The bank kingfishers (Alcedininae, c. 30 spp.) were primitively insectivorous and have specialised as perch- and even hover-diving piscivores; several became extratropical, and via Asia they have invaded Africa 6—8 times and America twice.

Aberdeen University, Aberdeen, Scotland, U.K.

Niches of *Turdus pilaris* and *Turdus merula;* how do they differ?

Robert K. Furrer

Sympatric populations of territorial *Turdus merula* (European Blackbird) and colonial *Turdus pilaris* (Fieldfare) have been studied mainly during the breeding season in central Switzerland. Both species have similar habitat requirements (cultural savannah, forest edge). Nest sites differ primarily in height above ground, but *T.p.* needs an open approach path for flying to the nest, whereas *T.m.* also uses sites that have to be approached on foot.

Food, as obtained by neck-collars from nestlings, shows great overlap, with earthworms constituting a major part. Direct observations also revealed similar foraging-habitat (open, short-cut meadows and freshly planted or fallow fields). In addition, *T.m.* forages to some still unknown extent inside of hedges and under the cover of trees. However, utilization of open foraging areas which seem of prime importance to *T.m.* as well, shows typical separation of the two species. *T.m.* generally forages considerably closer to cover than does *T.p.* Corresponding to the behavioral differences, *T.p.* shows adaptations to foraging farther from protective cover (disruptive coloration, greater wing length).

Schweiz. Vogelwarte, CH-6204 Sempach, Switzerland.

Photoperiodic Synchronization of Circannual Rhythms in European Starlings *(Sturnus vulgaris)*

Gabriele Gänshirt, John Dittami, Eberhard Gwinner

The annual cycle of gonadal function and molt in the starling are controlled by an endogenous circannual rhythmicity. Under constant environmental conditions these rhythms persist for several cycles with periods slightly different from 12 months. This raises the question of which Zeitgebers normally synchronize (entrain) circannual rhythms with the natural year. Since it is known that photoperiod exerts drastic effects on seasonal phenomena in many bird species, it was proposed that the annual cycle of photoperiod is a Zeitgeber of the starlings circannual rhythms. To test this hypothesis groups of male starlings were exposed to sinusoidal changes of photoperiod which simulated the natural photoperiodic changes in shape and amplitude, but differed in period. Cycles of 1, 3/4, 1/2, 1/3, 1/4, 1/5, 1/6, 1/7 and 1/8 year were used. The rhythms of testis size and molt in all birds followed the photoperiodic cycles down to 1/6 year. This indicates that the annual photoperiodic rhythm is, indeed, a Zeitgeber and that the range of periods to which these rhythms can be entrained is large. Within this range of entrainment the phase-relationship between the biological and Zeitgeber rhythms changed systematically as a function of the period of the latter, in a manner predicted by oscillator theory.—In a complementary experiment 5 groups of starlings were exposed to photoperiodic cycles which all had a one year duration but differed in amplitude, thus simulating the photoperiodic conditions of different latitudes. The results revealed differences between groups which are discussed in connection with the latitudinal differences in the timing of breeding cycles of free-living starlings.

(Supported by the Deutsche Forschungsgemeinschaft.)

Max-Planck-Institut für Verhaltensphysiologie, D-8131 Andechs, Germany.

Recent Outlines of Birds of Prey Ranges in the European Part of the U.S.S.R.

Vladimir M. Galushin

In the 30 years that have passed since the preparation of maps for vol. 1, "Birds of the Soviet Union" by G.P. Dementiev and N.A. Gladkov (1951) the ranges of many raptors has changed. Both range expansion and contractions have occurred. Some ranges are corrected due to more recent, precise data.

Some examples of range expansions are (among others); *Falco tinnunculus* (up to 67° at Kanin peninsula and the western coast of the White Sea), *F. vespertinus* (about 300 km to the north-west), *Circus pygargus* (up to 60° to the north), and *Hieraaei pennatus* (300—500 km expansion to the north-west).

Ranges have contracted of *Falco peregrinus* (extremely scarce south to tundra; disappeared from Baltic Republics, most of the Ukraine, northern Caucassus), *F. biarmicus* (the only known nesting place in Azerbaijan was deserted in the 1950s), *Milvus milvus* (no recent reliable record of nestings in the Caucassus), *Gyps fulvus* (disappeared from Moldavia

30—50 years ago), *Aegypius monachus* (disappeared from Moldavia 60—80 years ago), *H. leucoryphus* (no single nest to the west of Ural river; the species should be excluded from the list of nesting birds of the European part of the U.S.S.R. and of the Western Palearctic as well), *Aquila chrysaetos* (the southern limit is 300—500 km north to the former boundary), *A. heliaca* (the northern limit is 200—300 km to the south), *A. rapax* (the greatest retreat of the western limit to the east; about 800—1000 km from Moldavia to Stravropol district in the northern Caucassaus) and many others.

Only one new species is added to the list, i.e. *Falco sparverius*.

Moscow State Pedagogical Institute; U.S.S.R.

Mate selection in the European wren, *Troglodytes troglodytes*

Peter J. Garson

Male wrens hold territories throughout the year. During the breeding season males are typically polygynous, and they are solely responsible for building their several nests, which they show to prospecting females during courtship. The more nests that a male completes in a season the more breeding attempts he makes. Females usually make two breeding attempts per year and they normally switch mates between attempts.

How do females choose their breeding sites? Data are presented to show that the females show a preference for males with several complete but unoccupied nests in their territories, as opposed to those with only one. This preference is also related to the size of the males' territories. This result is explicable in terms of a random nest selection model for females.

Females, as a group, are therefore selecting males that are efficient at nest-building, but individual females are not exerting a choice in favour of such males. This implies that sexual selection has not had a significant effect on female mate choice, whilst it has selected for an increase in the amount of nest-building behaviour undertaken by males.

Edward Grey Institute and Animal Behaviour Research Group, Dept. of Zoology, University of Oxford, U.K.
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Unterschiedliche Zuggeschwindigkeiten nahe verwandter Vogelarten

Wulf Gatter

Schwärme rastender Vögel zeigen beim Abflug vielfältige Formen interspezifischer Vergesellschaftung. Während des Zuges kommt diese viel seltener vor. Truppzusammenhalt erfordert dabei gleichbleibendes Leistungsvermögen über lange Zeit hinweg. Wie Beobachtungen der Station Randecker Maar zeigen, scheint dies auch unter verwandten Arten nur selten vorhanden zu sein. So konnte hier immer wieder festgestellt werden, daß sich viele scheinbare Vergesellschaftungen nach kurzer Zeit lösen, weil eine Art schneller ist.

Am Randecker Maar (Schwäbische Alb) wurden auf einer gleichbleibenden Meßstrecke die Geschwindigkeiten ziehender Vögel gemessen. Günstige Bedingungen an der Station erlaubten es, über 2000 Messungen an vielen Vogelarten vorzunehmen. Dabei zeigte sich, daß innerhalb einer Gattung diejenige Art schneller fliegt, welche den größeren Handflügelindex-Wert aufweist. Meist handelt es sich dabei auch um die Art mit dem längeren Zugweg.

Dieses Ergebnis gab zu einer ganzen Reihe zugphysiologischer Überlegungen Anlaß. Sie werden am Beispiel von Buch- und Bergfink *(Fringilla coelebs* et *F. montifringilla)* behandelt. Von diesen beiden Arten liegen 266 unter gleichen Windbedingungen ermittelte Werte vor.

Station Randecker Maar — Vogelzug-Insektenwanderungen, 7318 Lenningen 3 — Schopfloch, Roßgasse 15.

Neotemperate (Texas) and Neotropical (Mexico) Avifaunas Near Their Geographic Limits: Seasonal Flux and Diversity

Frederick R. Gehlbach

Since an early investigation revealed the distinctively high, tropical diversity along the Río Corona, Tamaulipas, 300 km south of the Río Grande, Texas, I have continued to study both avifaunas. January (dry, non-breeding) and June (wet, breeding) seasons are compared. Temperature regimes are essentially the same; so is the tropical evergreen forest-type. Proportions of non-passerine and wintering, temperate zone birds and biomass are similar and characteristically tropical; but all species experience significantly less population flux on the Río Corona. This is also true at two other tropical sites in northeastern Mexico by contrast with two temperate sites on the Río Grande. Resident birds on the Río Corona show less seasonal shift in guild diversity compared to the Río Grande. Also, guild diversity is higher on the Río Corona and significantly correlated with greater metabolic efficiency in both seasons. Correspondingly, species' niches are narrower and more equitably dispersed. The higher annual precipitation, hence higher productivity, at the Río Corona may permit avian specialization on relatively fewer resources per species, if such resources are consistently available throughout the year.

Department of Biology, Baylor University, Waco, Texas, USA.

Individual and species specific song feature in Cardueline Finches

Hans R. Güttinger

In European and Asian species of Cardueline finches, I studied song variability among different geographic locations to determine if certain parameters of songs are consistent within a species and if there are any features that are consistent across different species.

The variability of song organisation in different dialect group within a single species revealed that the details of notes and the sequences of notes are probably modified by learning. In contrast to these variable features I also discovered a general song architecture, such as duration of the vocal pattern and relationship between vocal utterance and silent interval, that is remarkably consistent over all population of the same species.

I examined the songs of two species of Asian Greenfinches *(Chloris spinoides* and *Ch. sinica)* and Asian and European subspecies of the Goldfinch *(Carduelis carduelis)*, and found that the subspecies of the Goldfinch have an identical general song architecture which is different from that of the three species of Greenfinch.

I hypothesize that song learning is genetically preprogrammed for an individual; learned variation is limited to certain song features, such as the shape of notes, whereas the species specific general song architecture, such as the temporal pattern is genetically fixed.

Fachbereich Biologie der Universität Kaiserslautern, D-6750 Kaiserslautern, Germany.

Functional morphology and feeding behaviour of *Balaeniceps rex*.

Alfredo Guillet

Correlations of morphological differences with feeding behaviour are analysed following an approach developed for Ciconiiformes, combined with a novel computerised method originally developed for land surveying.

Museum skeletal material of Ardeaidae and Ciconiidae are employed as a reference base for comparative analysis with *B. rex* skeletal material and with information gathered from study of feeding behaviour in the wild.

Fitzpatrick Institute, University of Cape Town, Rondebosch 7700, South Africa.

Habitat and Conservation of the Shoebill Stork *(Balaeniceps rex.)*

Alfredo Guillet

The aims of this research are to:

1) Introduce some previously undescribed conservation problems with regard to the status of *B. rex* in the Southern Sudan's White Nile flooded valley;

2) compare sudden, artificially induced ecological disasters (e.g. the Jonglei canal) with longer term factors causing environmental degradation (e.g. swamp regression, fires, overgrazing, etc.);

3) outline those factors (particularly seasonal flood movements), which favour and limit this highly specialised species;

4) suggest a conservation programme which incorporates both ideal and obtainable measures.

Fitzpatrick Institute, University of Cape Town, Rondebosch 7700, South Africa.

Schalldruckpegelmessungen am Gesang des Teichrohrsängers *(Acrocephalus scirpaceus)*

Hubert Heuwinkel

Die unterschiedlich langen Lautfolgen beginnen mit einem leisen Anfangsteil. Der Hauptteil variiert wenig in Lautstärke und Tempo und endet abrupt. Die Laute enthalten ein bis mehrere Elemente.

Der mittlere Schalldruckpegel des Gesanges verschiedener Individuen schwankt zwischen 60 und 63 dB auf 3 m Entfernung im annähernd freien Schallfeld. Auf etwa 15 m Entfernung geht er in den Hintergrundgeräuschpegel über, wenn dieser ca. 45 bis 50 dB groß ist.

Im Vergleich zu anderen Arten ist der Teichrohrsängergesang als leise zu bezeichnen, seine Dynamik ist gering. Der Schalldruckpegel des Sumpfrohrsängergesanges beträgt auf 3 m Entfernung durchschnittlich 64,5 dB, des Schilfrohrsängergesanges auf 2,7 m 67,3 dB, des Drosselrohrsängergesanges auf 8,5 m 67,3 dB und des Zaunkönigesanges auf 5 m gar 71,3 dB.

Terzanalysen des Teichrohrsängergesanges zeigen, daß die lautesten Frequenzanteile der Elemente auf 2,21 bis 5,58 kHz entfallen. Das Frequenzspektrum ist damit verhältnismäßig tief.

Der über Lautsprecher abgestrahlte Gesang wird im Schilffeld auf 3 m Entfernung bis zu 5 dB gegenüber dem freien Schallfeld gedämpft.

Der Schalldruckpegel des Gesanges ist groß genug, um die Reviere akustisch verteidigen zu können.

Einzelne Teichrohrsänger erbringen hohe Imitationsleistungen. Ein untersuchtes Individuum imitiert Rufe 20 verschiedener Vogelarten.

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Song structure and territorial behaviour in european warblers *(Phylloscopus)*

Hans-Wolfgang Helb

The territorial function of the song of European warblers made it possible to find out the amount of territorial aggressiveness caused by the song, respectively its parts. Therefore play back experiments in field studies were used acoustically simulating rivalry.

Song structures changed in different ways showed distinctive differences in territorial behaviour. These data suggested to test if these structural possibilities of modification are deliberately used in the song production.

Results of the analysis of normal territorial songs (N) and aggressive "defending songs" (I):

Phylloscopus trochilus uses numerous possibilities to change its song depending on the situation. Compared to the normal song the intensive song I is, for example, characterized by shorter song intervals, an increase and temporal compression of the number of notes in each song, a temporal advanced and 1 kHz higher amplitude maximum and a reduced degree of variation. Immediately after the acoustic stimulation there can still be found a greatly different "transition song" showing territorial insecurity (U).

Phylloscopus collybita shows relatively slight structural changes. For song type I there are distinctively prolonged songs and a closer sequence of songs. Moreover there is an increase in the number of used note types with a higher maximum of the amplitude getting closer to the beginning of the song. Remarkable is the large increase in "trtt" calls.

The song structure of *Phylloscopus sibilatrix* does not vary much; There is a more compact sequence of notes within a song.

In territorial behaviour the calmer *Ph. trochilus* exhibits far a greater modification of song structure; *Ph. collybita* and *Ph. sibilatrix*, showing less acoustic flexibility, but are predominantly physically aggressive.

Fachbereich Biologie der Universität, Kaiserslautern, Germany.

The Role of the Reversionary Trends in the Descend of Birds

Lajos Horváth

If there occur in a species aberrations of a nature which arise as normal features in another species of the same genus, or in a higher category then the aberration accounts for a kind of relationship between the two species either by indicating that they descended from a common ancestor or that the progenitor of the species displaying this aberration is the one which possesses it as a regular feature. In the exposition and evaluation of the origin of the reversionary characters, we cannot rest content with the justified conclusion that the species under investigation is related to one or more species whose features occur on it in a decreased degrees, but we have to go further to arrive at the statement that the investigated species together with the one or more species whose features are common with it originated from an earlier common ancestor or ancestors. The higher the number, the extence and the intensity of the reversionary-aberrational characters are in a given species, so much later did it separate from the one or more species to whose features it reverts—therefore the

strength of the reversionary aberrations is conditional on the age of the species. My conclusions rest on investigations of many and very different sets.

Natural History Museum, Budapest, Hungary.

Anthropogenic changes of birds fauna

Ju. A. Isakov

Man transforms the majority of natural landscapes into anthropogenic (towns, fields etc.) and seminatural (pastures, secondary forests) ones. Different ecological groups of birds respond to natural changes differently. The number of bird species reared artificially and becoming synanthropic increases, their population augments, areas expand. Population of other species decreases or sometimes disappears altogether. The territory distribution of birds changes. The process of their urbanization develops: feeding and resting, nesting and wintering in towns, the change of daily rhytms, developing into sedentary state and year round breeding. The composition of fauna is supplemented by introduced, accidentally naturalized and synanthropic species settling in new places. Appearance of new ecological niches not yet occupied makes this process easier.

Unification of the main body of fauna, that is the group of the most numerous species on large territories trends towards impoverishment of its composition. In perspective the quantity of populations and their numbers of reared and synanthropic species sustained by man will increase as a result of the directed rise of capacity of their biotopes, number of synanthropic agricultural pest species (in proportion with economy intensification) will decrease; conservation of misanthropic species of the native fauna will be possible only within the refuges in natural and seminatural landscapes. All these ideas are in proved by numerous examples.

(Institute of Geography Academy of Sciences of the USSR, Moscow, USSR).

Birds' Group Orientation

V. E. Jacoby

Radar and visual observations of migratory birds show the presence of group or flock orientation by some bird species. Inter and intraflock signalization and communication has also been noted. Groups select the optimum migration route based on food, aerodynamics orientation by some bird species. Inter and intraflock signalization and communication has been noted. Groups select the optimum migration route based on food, aerodynamics and other conditions. It uses both experience and the accidental detection of these conditions by individual members of a flock or by separate flocks of a group. The extension of surveyed territory through the increase of the flight's altitude, of the size of the group and its potential orientation experience give the possibility of true navigation, when a large part of a group doesn't see a goal, but selects a correct flight direction by following

the few more experienced birds. At night signalization and communication are done by acustic means. The distance between flocks of a group and the size of a flock decreases when sparrow-like birds fly singly at distances of audibility. Such a dispersed group of birds tied together acustically may represent a wave of migratory birds stretching for tens and possibly even to hundreds of kms. Part of these birds can fly in complete cloudiness or in darkness orienting themselves on acustic signals of neighboring which can orientate themselves on stars or ground orientators.

Severtzow Institut, Moskau, U.S.S.R.

Numbers, Distribution and Movements of Flamingos *(Phoenicopterus ruber roseus)* in the Mediterranean and North-West Africa

Alan Roy Johnson

Data are given for the numbers and seasonal distribution of Greater Flamingos *Phoenicopterus ruber roseus*. The area under review extends from Guinea Bissau north along the Atlantic coast of North Africa and throughout the Mediterranean east as far as Iran. Three geographical zones are recognised within this vast area; the West African, the West Mediterranean and the East Mediterranean. It is not suggested that the populations of these are isolated; on the contrary ringing has proved that they are inter-related, particularly those of the two former zones. They are, however, separated geographically by distinct gaps in the breeding distribution of 2,000 kms or more and interchange is limited.

Counts have been carried out during the breeding season and in winter, more in the West Mediterranean than elsewhere, and population estimates are given. Movements as revealed by ringing recoveries are reviewed and knowledge is increasing rapidly by ringing with coloured leg-bands individually recognisable in the field which began in the Camargue in 1977.

Station Biologique, La Tour du Valat, Le Sambuc, 13200 Arles, France.

Angaben über die Biologie und Postembryonalentwicklung des Habichts *(Accipiter gentilis* L., *1758)*

Ladislau Kalabér

Nach kurzen Angaben über die Verbreitung in Europa und besonders in Rumänien werden, gestützt auf Beobachtungen an 18 Horsten, die Biotopansprüche, die Brutbiologie und die Ernährung in Rumänien behandelt. Veränderungen der ernährungsbiologischen Gegebenheiten scheinen die europäischen Habichtpopulationen besonders nachhaltig beeinflußt zu haben.

Daily and seasonal variation in the drinking flights of East African Sandgrouse

Heribert Kalchreuter

From July 1974 to June 1975 behaviour and population dynamics of *Pterocles exustus* and *P. decoratus* were studied in monthly intervals at Ngaserai/Northern Tanzania. The beginning of the daily drinking flights varied considerably and was closely correlated with the cloud cover. More than 50% overcast caused a delay of half an hour or more. The intensity of the flights depended on the availability of other water sources or heavy dew.

The flying and drinking activity was high from July to December, which coincides with the breeding season and the period of lowest rainfall. During rain season (peak March to May) the flights were still performed, but the birds just landed in the surroundings of the water, but very few only came to drink. In April/May especially *P. decoratus* did not perform noticeable drinking flights, only exhibited undirected flying activity during the usual flying time.

Arbeitsstelle für Wildforschung Baden-Württemberg, 7823 Bonndorf-Glashütte.

Determination of Origins of Waterfowl by X-Ray Spectrometry

John P. Kelsall

Results are reported of experimental work aimed at the resolution of problems and unknowns involved in the identifications of origins of waterfowl through computer-controlled, X-ray spectrometric analyses of primary flight feathers. Materials from wild and captive populations of lesser snow geese *(Chen caerulescens)* were used. New methodology, the use of an X-ray tube source of irradiation, was introduced to previously described techniques. Practical investigation of sample size for the generation diagnostic chemical profiles in the form of discriminant functions suggests that 40, or preferably more, samples per population should be used. Given adequate sample numbers, and suitably different populations, the processes of diagnosis of population characteristics and classification of unknowns, can override differences attributable to sex, age and year of feather growth with great accuracy. This technique for determining origins of geographically distinct populations could be applied to other birds, mammals and other animals. A selected bibliography of recent, relevant literature is included.

Canadian Wildlife Service, 5421 Robertson Road, DELTA, British Columbia, Canada. V4K 3N2.

Bird Sound Recordings in the British Library of Wildlife Sounds

Ron Kettle and Jeffery Boswall

The British Library of Wildlife Sounds contains thousands of bird sound recordings from all regions of the world. It comprises: 1. over 500 gramophone records and

cassettes which include the sounds of about 2,500 species of birds; 2. a duplicate copy of the BBC Sound Archives natural history recordings covering nearly 1,000 bird species; 3. tape recordings contributed by private recordists and other organisations of about 1,250 species. Detailed documentation accompanies each tape recording. The collection is available for research, and copies of tape recordings and most of the BBC recordings can be supplied for that purpose. More contributions are invited. Leaflets about BLOWS are available at the side of the poster.

British Institute of Recorded Sound, London, U.K.

Feather protein electrophoresis: a new technique in avian taxonomy

Alan G. Knox

Reduced and carboxymethylated keratins (SCMK) from the barbs of feathers from a number of species of birds were examined by electrophoresis in polyacrylamide gels. Very low levels of intra-individual and intra-specific variation in SCMK were found, but there were considerable differences in the electrophoretic patterns from all the well-defined species examined. The electrophoretic similarity (I) between pairs of species and Nei D values were calculated for some of the birds. There was a high degree of congruence between published classifications and the results obtained from the SCMK. The results show that SCMK has considerable potential as a source of avian taxonomic information, the ready availability of samples and the robustness of the procedures involved making this method very attractive.

Examples illustrating the range of inter- and intra-ordinal variation are given and results of taxonomic studies using feather protein are shown.

Department of Zoology, University of Aberdeen, Aberdeen, Scotland. U.K.

Autopreening and Allopreening in the Great Green Macaw (*Ara a. ambigua* Bechstein)

Klaus Kortstock

Autopreening and allopreening behaviour was studied in 14 captive birds. Daily observations indicated that preening activities occurred mainly two hours before sunset.

a) Preening events were quantified as to frequency of occurrence on 12 defined surface areas of the body (breast, back etc.).

For autopreening a direct relationship of 1 : 1 existed between the area of the plumage parts and the frequency of preening, except for the oil-gland, which was preened more often than predicted by surface area.

For allopreening we found no such relationship. Two relatively small areas, the cloaca and head, were allopreened most frequently.

b) The frequency of autopreening and allopreening of the different localities was compared.

The majority of allopreening events (52%) were directed toward areas easily preened by the recepient with its bill.

Therefore feather maintenance is probably not the only function of allopreening. Another function might be the maintenance of pair-bond.

c) During autopreening the transitions between preening elements were investigated.

Seldom was the same part of the body preened twice in succession. Transitions between some neighbouring localities, and between the oil-gland and wings and tail, occurred significantly more often than predicted by X^2.

The oil-glands of macaws are rather small. The function of the oil-gland is apparently taken over by powder down. The above pattern of preening has two possible explanations:

1. The tiny oil-gland is functional.

2. Oiling has remained in the behavioural repertoire as a relict.

Univ. Bielefeld, Lehrst. f. Verhaltensphysiol., 48 Bielefeld 1, Postfach 8640, Germany.

A hitherto unknown picture (late 16th century) of the Hermit Ibis, *Geronticus eremita* (L., *1758*) belonging to the former Alpine population died out in the first half of the 17th century. With a review on historical figures of the species from the 16th to the late 19th century.

Hans Kumerloeve

Scientifically described for the first time by Gessner 1555 as a breeding bird of the Alps, the Hermit Ibis disappeared here apparently during the third of fourth decennium of the 17th century. Only 4 to 5 figures seemed to be known from these times (Stumpff 1548?; Gessner 1555; Härtli, St. Galler Handschrift 1562; Hoefnagel um 1582/90; finally Albin 1740), and many later ornithologists believed in the following centuries that this bird never existed at all. In the year 1825 it was found in Near East by Hemprich & Ehrenberg, later also in Algeria (Loche 1867, Levaillant et al.), Morocco and in SE-Turkey (Danford 1879)—but without be identified with the Alpine Waldrapp!—, until Rothschild, Hartert & Kleinschmidt (1897) were able to prove the species-identity of those birds with the former European population. A short review on the figures published since Gessner till the end of 19th century is given here: culminating in the shortly found very typical picture of the "Österreichische Nationalbibliothek, Handschriftenabteilung" (Vienna) from the late 16th

century, presumably painted by Joris Hoefnagel and collaborators resp. members of his workshop. Further research on this problem will be necessary.

8032 Gräfelfing (München), Germany.

The Breeding Biology of *Collocalia fuciphaga*

N. P. E. Langham

A breeding colony comprising about 1,000 pairs of the Edible—nest Swiftlet, *Collocalia fuciphaga* was studied from September 1976 to April 1977. The colony was in a Chinese shophouse in Penang, West Malaysia (GRID. REF. Lat. 5°30′N., Long. 100°10′E.). Breeding occurred throughout the period of study with peak laying in October and February. 150 nests were marked for closer study.

The average clutch (1.93) varied little. Hatching success was 70.3%, fledging success was 61.4% with an overall breeding success of 43.3%. Breeding success declined with successive clutches in the same nest, from 46.5% initially, to 40.8% for second and 35.0% for third clutches, owing to nests falling or becoming inadequate to hold their contents.

Breeding was not directly correlated with rainfall, but the main appearance of young in the nest coincided with the end of the monsoon and the coming of the dry season. This period would have the greatest number of aerial arthropods. 13 foodballs examined showed Hymenoptera to be the most frequent prey, followed by Diptera, Ephemeroptera and Aranae with equal frequency.

Moult occurred throughout the study period; primary moult occurring in about 50% of the birds, except in November and December when less than 30% showed primary moult.

The University of the South Pacific, Suva; Fiji.

Winter territories in Townsend's Solitaire *(Myadestes townsendi)*

Roger J. Lederer

The Townsend's Solitaire *(Myadestes townsendi)* often maintains intraspecific feeding territories during the winter season. Territoriality is apparently facultative, as it does not always occur. The presence of territoriality is dependent upon 1) the distribution and abundance of food, 2) conspecific and other avian competitor populations, and 3) energy requirements imposed by climatic conditions. The sizes of the territories and time budgets are also dependent upon these factors.

On this study area in the Sierra Nevada of northeastern California, the solitaire eats only berries of the Western Juniper *(Juniperus occidentalis)*, a very important food source for a number of avian and non-avian species in the winter.

Dept. of Biological Sciences, California State University, Chico, Calif., USA.

Vocal Imitations of African Birds by the Marsh Warbler *Acrocephalus palustris*

Françoise Lemaire

This paper presents the first extensive evidence of vocal imitations of African birds by a Palaearctic migrant, the Marsh Warbler *Acrocephalus palustris*. Nearly 30 individual tape recorded repertoires have been analysed; imitations of each identified species were compared to models by spectrographic analysis. A list of 113 African species (33 non-passerines, 80 passerines) was thus established, which, added to the European list of 99 species, gives a total imitative range of 212 species.

Individuals imitate on average 76.2 different species (31.2 European +45.0 African species). About a fifth of the complete song remains unidentified and probably corresponds to imitations of African birds whose voices have not been recorded yet.

Vocal imitations of some rather local species in eastern Africa provide information on the localisation of the autumn and winter quarters of the Marsh Warblers. In particular, the frequency of imitations of such species as *Streptopelia vinacea*, *Cisticola bodessa* and *C. ruficeps* lends support to the idea of the existence of autumn quarters in north-eastern Africa.

Circumstantial evidence indicates that the young warblers probably stop learning soon after their arrival in their winter quarters, most of them during the month of January, at the age of six-seven months.

University of Liège, Belgium.

Exotic Birds in South Africa

Richard Liversidge

The number of exotic species released or escaped from captivity in Southern Africa is unknown. Some thirty species are known to have been deliberately introduced. Several species and in particular the "European" pheasant have been repeatedly reintroduced.

The only species that have successfully established themselves are those that live in close association with man and his environment. The possible exception to this is the rose ringed parakeet with which there is some doubt as to its origins.

Population development of successful species has followed a normal expotential growth curve. When this curve becomes vertical the threatening population explosion is accommodated by colonalisation of new areas. Limits of expansion appear to be caused by ecological factors where populations have become stable.

Possible reasons for lack of success in many introductions has been the large spectrum of predators.

McGegor Museum, Kimberley, South Africa.

Antarctic penguins: their strategy to live in the cold

Yvon le Maho et Bernard Despin

Seven species of penguins live and breed in the Antarctic region (along the coasts of the Antarctic continent and in the Sub-Antarctic area). To understand the adaptative strategy which allowed these species to live in the cold, we studied the temperature regulation of three species: the Gentoo, the King and the Emperor penguins; then we compared their ecology and behavior.

Because of their morphological and physiological adaptations, the lower critical temperature (the lowest air temperature where the metabolic rate may be maintained at its minimum value, the basal metabolic rate) is as low as about −5°C for the Gentoo and the King penguins; it is even much lower for the Emperor, about −10°C. In the Sub-Antarctic area, where the Gentoo and the King penguins breed during the winter, the ambient temperature never falls much below about −5°C. The Gentoo—because of its smaller size compared to the King (about 5—8 kg versus 10—18 kg)—may breed also during the short summer in Antarctica, while ambient temperatures are at or above −5°C.

The Emperor penguin breeds on the sea-ice, along the coasts of the Antarctic continent, at air temperatures between −10 and −50°C, thus well below its lower critical temperature. Nevertheless we found that social behavior (huddling) allows the emperor to keep up at the basal metabolic rate.

Thus, to maintain the resting metabolic rate at its basal value seems to be a fundamental aspect of the stategy of penguins to live and breed in the cold.

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Aspects of Recovery Strategy for Cached Seeds in the Thick-billed Nutcracker *Nucifraga caryocatactes caryocatactes*

Hermann Mattes

A Nutcracker can find its cached seeds under a thick cover of snow with the high rate of more than 80% of successful digging. Discovering strategy and way of orientation are still unknown. Probably the participation of memory is very high—no efficient searching pattern which could be used by the bird could be made sure or even likely—, but there is the difficulty to explain how a single bird can remember several thousands of depots.

Recovering power decreases slowly with increasing thickness of snow cover. It also is lower when the distance to probable orientation points is high. But there is no evidence of a constant distance or angle to any structure of the surface or to surrounding trees which could serve for visible orientation in a fixed searching pattern. The use of smell for primary orientation is unlikely because of the thick snow cover.

All suitable sites in the territory of the Thickbilled Nutcracker will be used for caching, specially snow-protected areas under dense tree canopies and on southern rocky slopes where the snow melts off soon. Depots within the territory are emptied not in a regular spacial order during winter, and rate of successful digging doesn't decrease at all.

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Seasonal variation of plumage and body weights of the American goldfinch, *Carduelis tristis*

Alexander Lewis Aitken Middleton

The American goldfinch acquires a dimorphic breeding (alternate) plumage that is significantly lighter than its winter (basic) plumage. The difference in weight is due to a lighter body plumage; abrasion of the flight feathers has a negligible effect. As the goldfinch does not nest until July, the existence of its pre-nuptial moult not only permits the acquisition of a strickingly dimorphic plumage, but also decreased plumage insulation which could be of advantage to a species nesting in the open during the height of the summer.

Although goldfinch body weights are at their heaviest in late January to early February an increase occurs in late April to May. This secondary peak occurs during the pre-nuptial moult, but also at a time when preparation for migration should be occurring. Carcass analysis showed that birds are at their fattest in January and February. The secondary increase in weight during April is related to an increase in the water content of the body and not to the deposition of fat. These results suggest that the secondary weight increase is a consequence of moult and not of migratory fat deposition.

Department of Zoology, University of Guelph, Guelph, Ontario, Canada.

The pineal organ of the house sparrow *(Passer domesticus)* —a neuroendocrine organ showing circadian activity—in tissue culture

Wilhelm Möller

Menaker and associates demonstrated the important role of the pineal organ of the house sparrow in circadian activities of the bird. In order to determine wether the pineal organ acts as an oscillator or as a neuroendocrine transducer these experiments were performed employing different culture techniques to study the activity and structure of the pineal organ without any neuronal and humoral interaction.

In organ cultures the organ center underwent degradation while at the same time the margins of the organ displayed normal ultrastructural features. Typical receptor like pinealocytes bearing an outer segment were not detected but even after long culture periods nerve cells could be demonstrated with the acetylcholine esterase reaction.

Using the Falck-Hillarp method serotonin production was demonstrated when 5-hydroxytryptophan was added to the culture medium but not after addition of tryptophan. Biochemically a twenty fold difference was found between the two experimental groups. This difference was correlated to the content of densecored granules (1,200 Å).

Using a perfusion and gasing equipment the central degeneration was reduced and serotonin was synthesized from tryptophan.

Successful cultivation of Vibratome esctions makes it possible to obtain several samples from one pineal organ for structural, morphometric and chemical analysis at different times.

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Long-term population dynamics in migrating passerines

Dieter Moritz

A severe decrease in the populations of several European passerines took place in 1969. To get more information concerning the qualitative and quantitative degree of normal fluctuations in bird numbers the figures of annual trapping and ringing on the island of Helgoland/German Bight are worked up.

Material: The annual totals of several migrating passerine species from 1953 up to 1978 (25 years). As field methods and equipment (funnel traps, mist nets) have not been especially prepared for quantitative studies during the first years some possible sources of errors are discussed.

The following details are regarded:

1. The degree of annual changes in numbers of trapped birds for a) irruptive species, b) partial and short distance migrants, c) long distance migrants.

2. The mean duration of populational cycles.

3. The possible correlation between figures of spring and autumn of the same year versa the correlation between autumn and subsequent spring.

4. Trends of short-, middle-, and long-term increase or decrease of populations in question.

5. The breeding area of migrants trapped on Helgoland as shown by ringing results.

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Territorialverhalten außerhalb des Brutterritoriums

Dieter Moritz

Territorialverhalten (TV) kennzeichnet jedes Territorium. Fälschlich wird es in seinen markantesten Ausprägungen oft als Indikator ausschließlich für Brutterritorien betrachtet. Territoriale Verhaltensweisen sind aber weder auf die Brutzeit noch auf das Brutterritorium beschränkt. Die Frage ist, in welchem qualitativen und quantitativen Umfang das der Brutzeit zugerechnete TV auch außerhalb des Brutterritoriums vorkommt.

Das Problem läßt sich dort behandeln, wo lokale Brutvögel nur einen geringen Prozentsatz des Artenspektrums ausmachen. Als Untersuchungsgebiet geeignet ist daher die Insel Helgoland, deren Brutvogelarten nur 4,4% der Artensumme stellen. 1976 und 1977 wurde vom 1. Januar bis 19. Juli (20 Dekaden) täglich das TV aller Gastvogelarten erfaßt und kategorisiert. Dieses Material wird mit dem Zugmuster der beteiligten Arten verglichen.

Ergebnisse: Von 166 Gastvogelarten zeigen 41 (davon 36 Passeres) TV, am häufigsten Gesang (98,7%). Bis Mitte Mai wachsen Diversität und Anzahl territorialer Arten. Dann nimmt zunächst nur die Diversität ab: Bei geringerer Artenzahl gibt es mehr Arten mit TV. Das ist ein Hinweis darauf, daß im interspezifischen Vergleich spät ziehende Arten noch auf dem Heimzug mehr TV produzieren als Frühzieher.

Intraspezifisch zeigen spätere Durchzügler mehr territoriale Aktivität als ihre früher ziehenden Artgenossen.

Diskutiert werden die biologische Bedeutung und die methodenkritischen Konsequenzen der Befunde.

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The wing and tail pterylosis in *Menura superba*

Maria L. Morlion

The wing and tail pterylosis of *Menura superba* was investigated using the clipping method.

On comparing the wing pterylosis of *Menura superba* with the one found in *Textor nigerrimus*, chosen as a representative of the Passeres, a great difference can be seen in the number of the different remiges and coverts, specially in those on the forearm. A very striking feature in the presence of eleven primaries as well as the presence of a series of primary upper lesser coverts in *Menura superba*. Another remarkable point is the great number of seconderies (14) and corresponding coverts.

For the tail pterylosis too a difference exists in the number of rectrices, greater upper and under tail coverts.

Rijksuniversiteit Gent, Laboratoria voor morfologie en systematiek.

Greater Cardiac Response to Hawk than to Goose Models in Naive Ducklings

Helmut C. Mueller

Heart rate response to the classical hawk-goose model was measured in 20 naive Mallard and 13 Pekin ducklings *(Anas platyrhynchos)*. Each duckling saw each model only once on successive days. Half saw the goose first and half saw the hawk first. The variance in heart rate for the 25 sec following model presentation was greater to the hawk than to the goose in 17 of 20 Mallards ($p = 0.0002$) and in 12 of 13 Pekins ($p = 0.0008$). Irregular heart rate is a good measure of fear and the data thus indicate that ducklings can recognize an aerial predator without prior, specific experience.

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Communal Roosting of Bald Eagles *(Haliaeetus leucocephalus)* in Desert Valleys of Utah, U.S.A.

Joseph R. Murphy and Kent Keller

During the period of approximately December 1—April 1 each year, large numbers of Northern Bald Eagles *(H. l. alascanus)* overwinter in the semi-arid valleys of northern and central Utah. It is thought that these birds represent a nesting population from parts of western and central Canada, which move south when prey populations become unavailable with the onset of winter. The conventional prey of this species (i.e. fish, waterfowl and other aquatic forms) are not available in these desert valleys, and the eagles are therefore dependent upon small mammals and carrion for food.

An important behavioral convention exhibited by the wintering eagles is the utilization of communal roosts, of which there are two basic types: (1) groves of deciduous trees in and around small farming communities on the valley floors, and (2) groups of coniferous trees in canyons in the nearby mountains. From these roost locations, eagles range throughout the broad intermontane valleys in search of food.

Speculation regarding the function of communal roost behavior centers around two major themes: (1) it is a means of ameliorating severe environmental conditions during winter, thereby enhancing survival for those birds utilizing the roost; (2) communal roosts provide for a form of information exchange or social facilitation whereby young, inexperienced eagles benefit from close association with adults that are more adept at finding and exploiting food resources during the winter.

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Flow around bird wing profiles made of poster paper

Werner Nachtigall und Ulrich Claussen

So far, abstractions about the flow around bird wings have only come from models. One chooses a technical profile resembling the cross-section of a bird wing and assumes

that the bird developes aerodynamical characteristic values (coefficients of lift and drag) similar to those of the model wing. However, bird wing profiles differ in many ways from the models, especially due to the extreme camber of the former. Therefor, the transferability is problematical. Using the profile measurement of pigeon wings presented by NACHTIGALL and WIESER (1966), geometrically similar plastic modells were built. The flow and separation phenomena of these modells were tested and filmed in a water tunnel as well as measured by an aerodynamical ballance in a wind tunnel. Characteristics of separation were obtained and could be investigated along the entire wing from one section to another. The aerodynamical polars of the individual wing sections are also characterised by the fact that, taken within the rage of critical Reynold's numbers, they often jumped from the subcritical to the supercritical rage.

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Activities of caged *E. schoeniclus* exposed to different artficial lights and temperatures

TSUKASA NAKAMURA

The experiment was conducted by exposing fifteen migratory *Emberiza schoeniclus* to different artficial temperatures in three chambers which were maintained at 23°C 15°C and 8°C respectively. Each chamber was lighted by two 15-Watt fluorescent lumps. The period of lighting increased from 9 hours to 15 hours and then, dicreased from 15 hours to 9 hours during the period from March through December in 1976.

The activities in the lighting period exposed to 23°C and 8°C increased mainly in May, June and July.

Whereas, the activities in 15°C increased only slightly in May and June.

The activities in the dark period, or Zugunruhe, increased both spring and fall migratory periods, and the group exposed to 15°C increased Zugunruhe only in spring period. Whereas, the group exposed to 8°C showed no Zugunruhe either in the spring or in the fall periods.

It can be said that the favorable temperature such as 23°C induced the onset of Zugunruhe in both spring and fall, and that 15°C induced Zugunruhe only in spring, but that low temperature such as 8°C inhibited the onset of Zugunruhe.

The results will be compared with comparable experiments with a few other passerine species.

Department of Biology, Yamanashi University Kofu, Japan.

Vogelschutzprobleme in Wäldern Litauens

ALGIRDAS NAVASAITIS

Durch intensive Entwässerungsarbeiten sind die Brutplätze u.a. von Kranich *(Grus grus)*, Schwarzstorch *(Ciconia nigra)* und Uhu *(Bubo bubo)* stark dezimiert worden.

Um die Brutgebiete vom Auerhuhn *(Tetrao urogallus)* werden Schongebiete gebildet, in denen Forstarbeiten von November bis Februar ruhen.

In der Nähe der Brutplätze vom Schwarzstorch, Kranich, Schlangenadler *(Circaetus gallicus)*, Fischadler *(Pandion haliaetus)* sollen von März bis September keine Forstarbeiten vorgenommen werden.

Die Durchforstungen, Pflegehiebe und Rückearbeiten werden noch in den Sommermonaten Mai bis September durchgeführt. Mit Rücksicht auf die Brutvögel sollten solche Arbeiten auf den Winter beschränkt werden. Wo die Bestände von Rabenkrähe, Elster und Kolkrabe zu hoch sind, sollte der Abschuß und die Zerstörung der Nester im April und Mai erfolgen.

Litauische Landwirtschaftsakademie, Kaunas, UdSSR.

Temperature sensitivity of the skin and temperature regulation in pigeons

Reinhold Necker

The temperature sensitivity of the skin plays an important role in temperature regulation of birds. It has long been assumed that different skin areas, e. g., naked or feathered parts, should have different thermal sensitivities. Investigations of the thermal sensitivity of different skin areas (effect of thermal stimulation of small areas on ongoing shivering) revealed that feathered skin areas are very important as thermosensitive areas for temperature regulation. The skin of the beak showed only a small sensitivity. No effect could be elicited with thermal stimulation of the unfeathered parts of the legs. Obviously the legs do not play a role as thermosensitive area; this is not in contradiction to the importance of the legs for heat dissipation. — Electrophysiological investigations have been done mainly in the trigeminal area. In pigeons cold receptors and warm receptors have been demonstrated in the skin of the beak. Because of the importance of the thermosensitivity of feathered parts electrophysiological recordings from cutaneous nerves were done. Sofar only cold receptors have been found in the skin of the wing. In recordings from dorsal horn neurones in the spinal cord (thermoafferent pathway) responses to cooling of the skin of the wings were found which support the existence of cold receptors in feathered skin areas.

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Function of a Wadden Sea Island (Schiermonnikoog) for some Passerines during autumn migration

Ebel Nieboer

In many cases the Wadden Sea Islands constitute the first land which Scandinavian birds encounter crossing the North Sea during autumn migration.

This poster presentation concerns the following mainly nocturnally migrating species, trapped by mistnetting in considerable numbers: Willow Warbler *Phylloscopus trochilus;* Pied Flycatcher *Ficedula hypoleuca;* Robin *Erithacus rubecula* and Goldcrest *Regulus regulus.*

The daily numbers trapped, represent in some respect the migratory intensity of the former night(s). Migratory intensity depends on favourable weather in Scandinavia and N.E. Russia.

Long-distance migrators (Willow Warbler, Pied Flycatcher) fly over the island in great majority if weather conditions are favourable there. Only some come down (drop out). If weather is bad the majority will interrupt (Fall).

Short-distance migrators (Robin, Goldcrest), do always come down after crossing the North Sea.

Visible subcutaneous fat (classification according to Busse c.s.) differs inter and intra-specifically at arrival. It increases during the course of the season. In general Willow Warblers arrive with a higher fat-class than Pied Flycatchers. Birds with low fat content stay longer than others at Schiermonnikoog. There is an increase in fat and weight in birds that remain after two days. However if weather is favourable long-distance migrators with few fat leave Schiermonnikoog too.

Biometrical comparison in combination with analysis of N. European weather conditions indicates a clinal increase in winglength in Robin and Goldcrest into N.E. direction.

Ring recoveries are a.o. from Norway, Sweden, Finland, Russia and Poland.

Biological laboratories, Free University (department of animal systematics and zoogeography), Amsterdam. The Netherlands.

Birds Seasonal Reproductive Cycle. External and Internal Factors

B. G. Novikov

The experiments have proved that birds seasonal reproductive cycle is based upon a deep interaction of internal and external factors. Hypothalamo-hypophyseal system being the major regulatory mechanisms of birds reproductive function, plays the leading role among all other internal factors. Evidence of both descriptive and experimental researches show that gonadotrophic functions of adenohypophysis is under control by the system of magno- and small-cellular nuclei of hypothalamus. Seasonal reproductive cycle is intimately bound with the special features of yearly rhythm of hypothalamic activity. Latter has to a certain extent an autonomous nature and in many instances fails to meet the feedback explanations. Comparative studies have showed that age changes in sexual cycle duration, its sexual asynchronity and final size of gonades are connected with genetically fixed peculiarities of hypothalamic activity. Ovulation and oviposition in different birds are bound with the diurnal cycle of respective hypothalamic nuclei and adenohypophysis cells.

In birds the reproduction cycle regulation depends on photoperiodism, which realize its influence through hypothalamo-hypophyseal system and synchronizes with the peculi-

arities of yearly and circadian rhythm of its work. This central regulatory mechanism has a wide evolutional flexibility that provides all variety of forms of adapting birds reproduction to the environment.

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Egg characteristics of passerines in North Finland

Mikko Ojanen

Egg size variations were studied near Oulu, North Finland in four passerine birds, *Parus major, Phoenicurus phoenicurus, Ficedula hypoleuca,* and *Sturnus vulgaris* in 1969—73.

Following results were obtained:

— Comparing data from different european populations no geographical trends were found in the egg size of these species.

— The egg dimensions of the Pied Flycatcher were not affected by clutch size. In the Great Tit and Starling egg size increased, but in the Redstart decreased with increasing clutch size.

— The laying sequence didn't affect the egg dimensions of these species with the exception of the Pied Flycatcher, in which it produced increasing egg volume in clutch sizes 6—8.

— The phenotypical correlations between female size and egg size were small in the Great Tit and Pied Flycatcher.

— The phenotypical effects of passerine female on egg dimensions were about 50—85 %. Different clutches of the same female during a year, the age of the female, and also temperature, which preceded laying, affected only slightly to the egg dimensions.

— The heritability of the egg size, calculated after mother-daughter pairs, was in the Great Tit 0.86 ± 0.29.

University of Oulu, Department of Zoology, Oulu, Finland.

The Conservation of the Aveiro Marsh

Nuno Gomes Oliveira

The main scope of this poster-presentation lies on calling the attention of the participants on the XVII Congressus Internationalis Ornithologicus for the need of preservation of the Aveiro Marsh, a vast wetland with international importance for waterfowl.

The Aveiro Marsh and its subsidiary hydrological system as well as dunes, woods and lagoons surrounding it, constitutes an important place for the wintering of waterfowl.

Last winter we have organized aerial countings in the marshland, with the following most relevant results:

Limosa limosa 2.000
Recurvirostra avosetta 1.000
Other waders 12.000
Melanitta nigra 6.500

The importance of the several ecosystems forming a so remarkable assemblage and some urgent measures for its conservation, as the creation of some Natural Reserve zones' (or even Integral Reserves), the control of hunting and motorized sports, the elemination of the pollution originated by two celulose factories, etc., are just some of the aspects focused in the present work.

On other hand, the need of prevent the concreteness of some truly disastrous works projected for the zone, as the construction of a dike-rood sliting the Aveiro Marsh in two, the drainage of some parts of the marshland, the transformation of natural lagoons for turism purposes, the urban invasion, etc., are just other problems deserving a general attention.

A law proclaimed by the Portuguese Governement in 1975 concerning the protection of the zone was avered insuficient. There is an urgence about very concret measures for saving a zone that can be considerated of international patrimony.

The words pronounced by the Count Lippens about the Marismas of the Guadalquivir can be repeated about the Aveiro Marsh—it is so absurd to dry the Aveiro Marsh for rice sowing, as it would be to demolish the Cathedral of Chartres for potato planting.

The Portuguese Center for Wildlife Study and Protection and the Portuguese Ornithological Congres; Porto, Portugal.

Census of breeding birds by the mapping method: a methodological study

Paul Opdam & Rien Reijnen

In The Netherlands ornithological data are being used more and more in physical planning ecology. For this purpose it has been necessary to census, by the mapping method, breeding bird territories over very extensive areas (sometimes up to 1000 km² or more) in one single year. Unfortunately too few observers were engaged. Consequently census data were seriously biased, not only because numbers of breeding pairs were undercounted, but also because one species was underestimated more seriously than another.

Thus far there exists no estimation of accuracy of the mapping method under given conditions. This study aims to determine census results of a series of woodland species, which are among the most difficult to count, in different parts of the year, at different hours of the day and in various types of forest. Once the specific census yield under standardized conditions is known, it must be possible to approximate total number of breeding territories of a species with the help of correction factors from the results of a few counts scattered throughout the breeding season.

Research Institute for Nature Management, Leersum, The Netherlands.

Hovering Flight—Types of Wing Motion and some Aerodynamic Problems

Hans Oehme, Holger H. Dathe, Ursula Kitzler

Two types of wing motion can be found in hovering birds. The lifting forces balancing the bird's weight are produced either by downstroke and upstroke or by the downstroke only. Both types occur in small species (e.g. Hummingbird, Redstart) and in larger ones (e.g. Pigeon, Jackdaw). It is shown that calculation of power output in hovering flight should not be based on the plain relations of an actuator disk neglecting the peculiarities of wing motion in space and time. Among other things attention should be paid to the uncertainty of the presence of steady state conditions. Further the very high lift coefficients necessary for a power calculation deviate from the properties of customary airfoils the more so as stalling of the wings while hovering seems to be not unusual.

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Zoogeography and Ecological Study of Black Woodpecker *(Dryocopus martius martius)*

Ko Ogasawara

Although Black Woodpecker has inhabited only in Hokkaido, Japan, Kawaguchi (1935) newly captured the above species in Mt. Hachimantai, northern Honshiu, Japan. After that, this woodpecker has not found in anyplace of Honshiu for a long time, but Shoji (1970) recently found a nest in Mt. Moriyoshi, Akita. By old published records, Ono (1803) reported that this woodpecker had inhabited in Sendai, Nikko, and Yamagata, northern Honshiu.

These facts are very important to the discussion of geographical distribution of birds.

By ecological study of Black Woodpecker in *Fagus crenata* forest, density (1.67 per ha) of used-tree which is classified into nesting, roosting, and feeding trees was almost the same as one of Hokkaido (Arisawa 1976).

Woodpecker has most frequently used the old big trees for feeding, and selected a favorable nesting and roosting trees. If nesting tree was older, woodpecker would used it as feeding tree. Furthermore, we speculated that this nesting tree would become roosting tree as if woodpecker excavated several holes on nesting tree.

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Autumn Migration of Water Birds on the North Coast of Sinai

Yoel Paran and Uzi Paz

Moreau's classical summary of migration across the Mediterranean (Ibis, 1961) postulates a mainly broad-front movement. The eastern end of the Mediterranean, on the north coast

of Sinai, with its massive diurnal movement of water birds, is especially well suited for a quantitative study of migration.

The birds, about 65% Garganey *Anas querquedula,* appear to coast along the shore, but there is a marked increase in the migratory stream from east to west. This phenomenon was quantified in September 1974 when 7 observation points were deployed at equal intervals along a 120 km stretch of the coastline. The records show an almost linear increase from east to west in the number of birds observed.

The facts seem to indicate a broad-front migration of equal density from north to south across the entire width of the eastern Mediterranean, possibly originating on the south coast of Anatolia. As the birds approach Sinai, the shore acts as a line of diversion. The birds are reluctant to cross the shore, change direction to the west and continue coasting up to the Bardawil Lagoon, which serves as a resting place for most of them.

Visual and some radar observations of arrivals coming in from the north (the sea) and veering to the west confirm the deductions reached from the statistical treatment of the numerical data.

Israel Nature Reserve Authority, Tel Aviv, Israel.

Bipolar Migration of South Polar Skuas

David Freeland Parmelee and David Rothwell Neilson

Under the auspices of the National Science Foundation, Parmelee is currently investigating the ecology and behavioral biology of several charadriiform birds near the United States' Palmer Station (64°46′ S/64°03′ W) on Anvers Island off the Antarctic Peninsula. The Palmer area is particularly attractive because it is a common breeding ground for two skuas, notably South Polar Skua *(Catharacta maccormicki)* and Brown Skua *(C. lonnbergi)*. Neilson is concentrating on interbreeding behavior in the two skuas, and how each differs ecologically on the breeding and feeding grounds. Unlike many resident birds of Anvers Island, both skuas leave the region for the austral winter period. To date there are no banding returns beyond the study area for Palmer-banded *C. lonnbergi*. Several recoveries of young *C. maccormicki* of known age and parentage are remarkable. Four banded by Neilson were recovered in the Pacific region at Baja California, and in the Atlantic region at Brazil (two recoveries) and as far north as 64° in West Greenland. Unbanded and formerly misidentified museum specimens from Greenland and the United States substantiate the investigators' belief that *C. maccormicki* regularly crosses the Drake Passage from Antarctica and flies northward along both coasts of the Americas to high latitudes in the Atlantic, and probably the Pacific.

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Theoretical and Practical Aspects of the Close Studies Concerning the Migration of Birds in the Lithuanian SSR

A. K. Petraitis and M. M. Zalakevicius

Systematic investigation of bird migration by visual methods began in Lithuania early in the fifth decade. Species composition and density of the spring and autumn migrants near the Bay Kursiu, Mares, was determined. The use of radar and other new methods was begun in the first half of the seventh decade to solve the problem of preventing the collision of planes with birds.

The dynamics of seasonal migration over this area were influenced to an important degree by seasonal weather factors. Through the territory of the republic, being on the flight path of birds (White Sea—Baltic Sea), the main stream of migration comes at high altitudes during good weather.

The spring and autumn flight of birds comes as a large front, but a concentration of birds is found in the Baltic littoral. In spring, members of the waterfowl complex (swans, wild ducks, curlews) predominate and during the autumn dendrophilic species (passerines, doves) do so.

During migratory periods birds pass through the area in waves. The intensity of flight in low and high layers of air does not always coincide.

The main flight of birds is usually in the first four hours in the morning.

The investigation of migration creates a scientific base for the appearance of crowds of birds on the itineraries of planes in different seasons of the year.

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Geographic and Seasonal Variation of Circadian Rhythms in Redpolls *(Carduelis flammea Subspp.)*

Hermann Pohl*) and George C. West**)

The phase relations between the daily (circadian) rhythm of cage activity and the natural light-dark (LD) cycle was studied in two subspecies of Redpolls: one from interior Alaska (ca. 65° N lat.), the other one from middle Europe (ca. 49° N lat.). Birds of each subspecies were transferred to the respective latitude of the other subspecies and were studied indoors together with the native population. The differences in the phase relationships between day activity and the LD cycle between the two geographical races were more pronounced in the Subarctic than in middle Europe, especially during midsummer and midwinter when the light conditions (twilights, photoperiod, range of LD cycle) are different at the two latitudes. The two subspecies could also be distinguished by the amount and duration of night activity („zugunruhe") at various times of the year. It was found that both, the actual light conditions at the respective latitudes and endogenous factors determine the phases of the activity rhythms with respect to the daily and annual solar cycle. The

significance of genetically determined functions was particularly evident in the phasing of the rhythms in two northern (circumpolar) populations of the same subspecies *(C. f. flammea)* that are adapted to different climatic conditions in Alaska and northern Fennoscandia.

(Supported by the Deutsche Forschungsgemeinschaft).

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Role of USSR Reserves in Protection of Rare Birds

S. G. Priklonski

In the Soviet Union at the beginning of 1978 there were 120 reserves with a total area of about 8.9 million hectares (0.4 percent of the USSR territory). Out of 766 bird species in the checklist for the Soviet Union 662 species are recorded in the reserves. Out of 63 rare and endangered bird species listed in the USSR Red Data Book only 3 species are absent in the reserves. Habitats and nesting grounds of the others are represented on protected lands. Usually they are most important (or sometimes the only known) nesting, moulting, wintering and migrative places for rare species.

Practically all nesting and wintering sites for *Phoenicopterus roseus,* the most of them for *Pelecanus onocrotalus, P. crispus, Porphirio porphirio, Lyrurus molokosiewiczi* and about 25 percent of them for *Aix galericulata, Francolinus francolinus, Otis tarda, O. tetrax* are situated in the reserves. The rare species with huge ranges are found in many reserves: *Ciconia nigra* in 73, *Haliaeetus albicilla* in 61, *Pandion haliaetus* in 58, *Falco peregrinus* in 20, *Circaetus ferox* and *Aquila chrysaetos* in 18 each.

Oka State Reserve, Ryazan District, U.S.S.R.

Migrational Strategies of three European Thrushes

Ruth Raiss

During their spring and autumn migration Redwings *(Turdus iliacus)*, Songthrushes *(Turdus philomelos)* and European Blackbirds *(Turdus merula)* rest on the island Helgoland.

An external estimation of four fat degrees, developped for rapid application, provides a satisfying field measure for the total fat content of migrating individuals. This and the recapture rate, duration of rest, body weight development and death rate give information about the resting behaviour, weather sensitivity and the physiological state of the birds.

A high mortality in unfavourable weather conditions as well as more and heavier weight losses during rest indicate a remarkable weather sensitivity in Redwings. Blackbirds however with relatively stable and rising body weight progress and in all conditions a low death rate are far less weather dependent, Songthrushes being intermediate.

According to studies of gizzard contents and food deprivation Blackbirds appearently dispose of the broadest feeding range while during starvation the utilization of a mixed diet appears lowest in Redwings.

The results are discussed as indicating different ecological strategies of migration.

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An Example of tool-use in the Rook, *Corvus frugilegus frugilegus*

James B. Reid

A new instance of avian tool-use is described. A young, captive Rook, *Corvus frugilegus frugilegus,* has been observed inserting a plug into one of six plug holes in an aviary, in order that water from a constant source accumulates on the aviary floor. This water is then used by all four birds in the aviary for drinking and bathing in. Evidence is presented showing that the bird involved is highly selective as to the choice of hole in which to insert the plug. The early development of this tool-using behaviour was not observed, so that causal factors in its ontogeny remain uncertain. Subsequent observations have revealed no correlations between the occurrence of this behaviour and various meteorological conditions prevailing when it occurs. The significance of the fact that the performer of the act is a young bird is discussed in the light of similar observations by other authors in this area, attention being drawn to the relationship between tool-use and play, exploration and ecological factors.

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Dachverband Deutscher Avifaunisten (DDA)

Goetz Rheinwald

1970 wurde — mit Unterstützung der Deutschen Ornithologen-Gesellschaft — der Dachverband Deutscher Avifaunisten mit Sitz in Radolfzell gegründet. Er besteht aus feldornithologisch tätigen Regionalverbänden mit mindestens 30 Mitgliedern sowie fördernden Mitgliedern. Sein Zweck ist die Förderung der Feldornithologie insbesondere der Avifaunistik auf wissenschaftlicher Grundlage, wozu besonders überregionale Kontakte, Koordination von Gemeinschaftsaufgaben, Herausgabe eines Referateorgans und Einrichtung eines zentralen Dokumentations- und Informationsdienstes gehören. Wesentliche Leistungen sind:

a) Herausgabe der „Ornithologischen Schriftenschau" mit etwa 3 Heften pro Jahr, in denen das europäische und großenteils außereuropäische Schrifttum referiert wird, wobei insbesonders Arbeiten über Faunistik, Vogelschutz, Ökologie und Ethologie im Vordergrund stehen;

b) Erstellung einheitlicher Manuskriptrichtlinien für ornithologische Publikationen in Zeitschriften der Bundesrepublik Deutschland;

c) Herausgabe der „Praktischen Vogelkunde" als methodischer Leitfaden für Feldornithologen;

d) Herausgabe des „Atlas der Brutverbreitung westdeutscher Vogelarten" nach einer Kartierung 1975 auf 50 × 50 km-Basis;

e) Gründung einer Seltenheitenkommission.

Auf den jährlichen Mitgliederversammlungen werden Themen der regionalen und überregionalen Arbeit vorgetragen und diskutiert. Daraus resultieren Empfehlungen für die weitere Tätigkeit, z. B. graphische Darstellung von Zug- und Beobachtungsdaten, Erstellung „Roter Listen", Rasterkartierung der Brutverbreitung, Biometrie- und Mauserkarten, Monitorprogramm, Bestandserfassung ausgewählter Vogelarten, Kartierung ornithologisch wertvoller Gebiete, Methodenkritik und Vogelschutz.

Derzeit gibt es 23 Mitgliedsverbände, die sich über den größten Teil der Bundesrepublik Deutschland erstrecken. In ihnen sind angenähert 2000 Avifaunisten organisiert.

Bonn, Germany.

Monitoring Bird Population Changes in North America

Chandler S. Robbins

The U. S. Fish and Wildlife Service and the Canadian Wildlife Service, with the help of 1,800 volunteer observers, have been conducting an annual Breeding Bird Survey since 1966. The main purpose of this survey is to monitor bird population changes. Within each one-degree block of latitude and longitude 2 or more (maximum 16) randomly distributed 50-stop roadside counts are conducted once each June. The stops are 0.8 km apart, and at each stop all birds detected in 3 minutes within a distance of 0.4 km are counted.

Computer analysis of the results by physiographic regions detects significant short-term and long-term changes in breeding populations. Many short-term increases and decreases are correlated with unusual weather conditions, especially severe winter weather, mild winter weather or prolonged rain during the breeding season. Many long-term changes are associated with spread of exotic species, range expansion of native species, and changes in agricultural practices. Maps showing breeding distribution and abundance of many species throughout the United States and southern Canada also are generated by the computer.

U. S. Fish and Wildlife Service, Laurel, Maryland, U.S.A. 20811.

Thermo-responsive neurons in the hypothalamus of pigeon

Gerhard Rosner

The activity of thermo-responsive neurons from the anterior part of hypothalamus have been recorded while cooling or warming the skin and/or the spinal cord. Altogether, the

number of units, whose discharge rate was distinctly dependent upon one or both of these temperatures, was about 25%. A total of 51 such neurons was found. From these neurons 38 (75%) were classified as warm-responsive and 13 (25%) as cold-responsive.

The neurons changed their impulse frequency rapidly during dynamic stimulation, but no overshoot was observed in all cases. The slope of static curves of neurons responsive to spinal warming were low in the temperature range of 30°C—40°C or 42°C and increased steeply at about 40°C. Neurons responsive to spinal cooling had slight changes in their slopes, and their activity ceases when spinal temperature reached 42°C to 45°C. The mean static curve of neurons responsive to spinal warming and the mean static curve of neurons responsive to spinal cooling intersected at about 38°C.

Two types of neurons responding to both skin and spinal cord stimulation could be distinguised: Type I, was excited by warming and type II, by cooling both skin and spinal cord. A neuron which responded to cold skin and warm spinal cord or reverse was not found.

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Biophysical and Bioenergetical Aspects of the Flight of *Columba livia* in a Wind Tunnel

Hans-Joachim Rothe und Werner Nachtigall

A new wind-tunnel for experiments with medium sized birds is presented, photographs of pigeons flying in the tunnel are shown. The tunnel is 9 m long, the area for bird flight is 1 m² in cross section and 1,4 m long. The latter can be replaced by a tiltable section (tiltable from −20° to +20°). The maximum air speed is 25 m/sec. The time a pigeon requires to learn flying in the tunnel and the different training periods which are necessary for it to learn are shown in diagrams. During the training the pigeon improves its flying technique so that the loss of weight caused by the loss of water and by the energy production is minimized the longer the pigeon is trained. Having learned to fly in the most economical manner, the loss of weight only depends on the wind speed, the ambient temperature and the flight angle which was generally 0° in our experiments. Training has a similar influence on the skin and cloaca temperature. If the pigeon is not well trained skin and cloaca temperature rise very quickly and the bird starts panting after a short period of flight. If the pigeon is well trained and in good condition, its temperature climbs up to a point of steady state and panting seldom appears.

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Co-operative feeding by Splendid Wrens, *Malurus splendens*

Ian Rowley

A study of Splendid Wrens on Gooseberry Hill close to Perth has shown that most aspects of its ecology and behaviour are like those of *M. cyaneus* of the eastern side of the con-

tinent, which I reported on more than ten years ago (Rowley, Emu 1965). *M. splendens* differs in one important regard—the female offspring as well as the male, may persist in the family group and assist in rearing the young. This never happened with *M. cyaneus* with the result that differential dispersal and the consequent sex imbalance have been held to be largely responsible for co-operative breeding in *Malurus*.

Over five years, seven out of 48 group/years had more than one female in them. The helper female did not incubate but she helped equally with other group members in the feeding of nestlings, in nest sanitation by removal of faecal sacs, and the care of the young after they have left the nest.

The study area has been repeatedly burnt and the consequent declining quality of the habitat has been exacerbated by two very dry years. The area of suitable habitat has been reduced and this has depressed dispersal and has led to larger groups with „helpers" of both sexes amicably rearing young under extremely adverse conditions.

C.S.I.R.O., Division of Wildlife Research, Helena Valley, Western Australia.

Social organisation and the use of crèches in the galah, *Cacatua roseicapilla*

Ian Rowley

These cockatoos nest in hollow trees and a pair will drive off conspecifics from within 3 metres of the nest-hole. Both parents incubate, brood and feed the nestlings; they forage nearby with other locally breeding pairs. The eggs hatch asynchronously and the young fledge successively; their first flight generally exceeds 1 km and ends in trees where other fledglings forgather and a crèche is formed. Young remain in the crèche 7—10 days whilst their siblings fledge and join them; they practise flying and are fed by commuting parents. After the family is reunited, it leaves the crèche and moves nearer to the food supply—usually spilt wheat; juveniles begin to join their parents on the ground and soon start to feed themselves. When the young have been six weeks out of the nest, the parents desert them, return to their nesting area and start to moult, resuming their circumscribed residential existence and roosting each night near the nest tree. First year juveniles disperse widely in peer-flocks but in subsequent years they tend to join a local immature flock which forages over a large home-range and from which recruitment to the breeding population is made. Most galahs breed first in their fourth year.

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Ratite Eggshells from Mio-Pliocene-Continental (mpC) Sediments in Southern Morocco

E. G. Franz Sauer and Eleonore M. Sauer

Ratite eggshell remains were recovered, in 1974 and 1976, from mpC-sediments (76 newly discovered sites) in the Khela syncline between the High Atlas and Anti Atlas. The

fragments were identified, primarily, by their pore patterns which included aepyornithoid, struthious, and intermediate types. The latter contained aepyornithoid and struthious pore characters in various degree of expression and appeared to represent phylogenetic links between the two main types, corresponding with a gradual disappearance of the aepyornithoid traits.

Pores, rows of pores, pore complexes, grooves, microgrooves, pore densities and the shell thickness were measured and subjected to statistical analyses. The shell thickness ranged, on the average, from 1.46 to 2.65 mm (min. 1.40; max. 2.70 mm) and was positively correlated with the pore density, although a poor fit of the data to a linear line of regression suggested that the traits were transmitted independently.

Sizes, volumes, and shapes of eggshells were calculated from measurements of the cardinal curvatures of the relics. Some of the eggs were ellipsoid, comparable with recent struthious eggs; deviations revealed a trend toward an ovate type as seen in aepyornithid specimens. The largest reconstructed eggshell had a volume of 2216.1 cm^3, i.e. 56.5% larger than the largest of 169 eggs from *S. c. australis.*

The ratite eggshell remains from southern Morocco were phylogenetically linked with aepyornithoid eggshells from the Miocene and Pliocene of Anatolia and with aepyornithoid and struthious eggs from the Mio-Pliocene of Lanzarote, Canary Islands.

Zoological Research Institute and Museum A. Koenig, Bonn, Germany.

Breeding behavior in the tree swallow

Charles R. Schmid

Behavior details during the breeding season of a tree swallow which arrived each breeding season as a female, exhibited perfect tree swallow female behavior, (obtaining a male mate, building her nest, copulating, etc.) and then, suddenly reverting to perfect tree swallow male behavior, obtaining a male mate, siring and raising and fledging young, etc. Observations made at a 40 nest-box tree colony on Cape Cod, N. Truro, Massachusetts. USA. Autopsy confirmed observed behavior.

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Instrumental Thermoregulatory Behavior in the Pigeon*)

Ingrid Schmidt**)

Pigeons exposed to thermal loads quickly learn to interrupt a photo-gate with their heads, if this instrumental response is followed by a reduction of the thermal load (rein-

forcement). When confronted with ambient heat loads between 40 and 60 °C and provided with sufficient reinforcement-magnitudes, they maintain deep body temperatures stable without employing increased respiratory heat dissipation. This results in a linear increase of the response rate for cooling reinforcement with the heat load keeping the temporary mean of ambient temperature constant. When the efficiency of behavioral thermoregulation is limited by reducing the reinforcement-magnitude, the animals do not increase the response rate to such an extent as to prevent rises in body temperature, and subsequent activation of autonomic heat defence occurs. Provided reinforcement-magnitude is sufficient, the instrumental response rate is rapidly adjusted to changes of external heat load without preceding changes of core temperatures or skin temperatures at densely feathered areas indicating the importance of exposed regions in the control of behavioral thermoregulation. Experimental variations of central temperatures affect both, behavioral and autonomic effectors, resulting in changes of their contributions to overall thermoregulation under the given peripheral heat load.

*) Supported by the DFG (SFB 114).
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Der Wintervogel- und Sommervogelbestand der Nordseeinsel Borkum

Erich Schoennagel

Die 32 km² große Nordseeinsel Borkum habe ich in 20 Zählstrecken eingeteilt. Vom Oktober 1976 bis zum September 1977 habe ich auf rund 250 Tagesexkursionen in jedem Monat durch Linientaxierung den gesamten Vogelbestand der Insel qualitativ und quantitativ aufgenommen. Das Ergebnis habe ich — nach dem zoologischen System geordnet — in 3 Tabellen dargestellt:

1. Wintervogelbestand
2. Sommervogelbestand
3. Winter + Sommervogelbestand.

Den Tabellen ist für jede beobachtete Vogelart die Jahreszeitliche Bestandsfluktuation zu entnehmen. Ferner ersieht man, in welcher Anzahl die einzelnen Vogelarten in jedem Monat auftreten.

Den höchsten Bestand an Individuen weist der September (208.623 Ex.), den niedrigsten der Juni (19.081 Ex.) auf. Insgesamt wurden 167 Arten und 3 Rassen mit 586.601 Exemplaren notiert. Selbstverständlich überwiegen zahlenmäßig die Limikolen.

Die Diskussion möge ergeben, welche Zählmethoden zu besseren Egebnissen und zu einer besseren Darstellung führen.

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Reproductive success of the Brown Pelican *Pelecanus occidentalis* during 8 years, 1969—1976, in Pinellas County, Florida

Ralph W. Schreiber

Data on clutch size, hatching success, and fledging success for eight consecutive breeding seasons are presented. Seasonal variability in nesting success, the effects of clutch size on nesting success, the amount of relaying, and annual fluctuations in productivity are compared. Figures calculated from various methods of measuring productivity (three visits per week to nests, weekly visits, counts of maximum number of nests and maximum number of young present, and counts of young per nest) indicate important differences in productivity based on the method of investigation and the amount of human disturbance. The implication of these findings to other productivity studies of birds are discussed. The results of this field study are compared to the theoretical "recruitment standard" for this endangered species.

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Status und Veränderung des Weißstorch-Bestandes
Status and Trend of the White Stork Populations

Ernst Schüz

III. Internationale Bestandsaufnahme des Weißstorchs 1974 (Third International Census of the White Stork 1974 under the Auspices of I. C. B. P.)

Solche Bestandsaufnahmen durch zahlreiche Einzelbearbeiter und Institute in Europa, Afrika und Asien fanden 1934, 1958 und 1974 statt. In Europa etwa 90- bis 95000 Brutpaare (HPa); Individuenzahl beim Wegzug (mit Nichtbrütern und Jungen) etwa HPa × 5. Besonders im W starker Rückgang. Von 27 Staaten (UdSSR als 1 Staat gerechnet) beteiligten sich 23 am Zensus 1974: In 14 Abnahme, in 6 Trend unsicher, in 3 Zunahme. Auf deutschem Boden (heutige Grenzen) Rückgang von 9035 (1934) auf 4000 (1974); Verlust 56 % (Bundesrepublik Deutschland 76 %, Deutsche Demokratische Republik 37 %). — Bei hohem Anteil von Spätankömmlingen (meist = jungenlose Paare, HPo, wechselnd zwischen 7 und 72 % an HPa) „Störungsjahre" mit schlechten Brutergebnissen; alle Übergänge bis zu „Bestjahren". Wichtig das Nahrungsangebot bei der Aufzucht: Benachteiligte Junge (Spätschlüpfer) bilden eine Reserve, die selten ganz durchkommt, sonst dezimiert wird („Kronismus" durch die Eltern). Darmparasiten, Wetterkatastrophen (diese auch auf dem Zug), Nahrungsmangel (meist wetterbedingt), Störenfriede bilden die naturgemäßen Gefahren. Hinzu kommen die vom Menschen verschuldeten Schäden: Grundwassersenkung, Verbauung, technische Unfallgefahren (Verdrahtung usw.), Nistbehinderung, Biozide, außerhalb des Brutgebiets Fang und Abschuß für Nahrungszwecke usw. — Der Weißstorch, Indikator der Umweltgüte, wird immer mehr Opfer der Technisierung. Arbeitsgruppen in vielen Ländern werben und legen Hand an für den Schutz des Storchs; in Schweiz und Elsaß versucht man Wiederansiedlung.

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Birds and Sugars: Starlings Prefer Glucose and Fructose but Reject Sucrose

Werner Schuler

Some species of birds (e.g. honeycreepers and amazons) select solutions of sugars over pure water, others (e.g. siskin and redwinged blackbird) reject them. These findings lead to the idea, that nectar and fruit-eating species prefer sugars, whereas insectivorous and granivorous species reject them or behave indifferently. Preference behaviour of the European starling *(Sturnus vulgaris)*, a species which eats insects as well as fruits, was tested in two-bottle drinking tests with water and sugar solutions. Starlings preferred higher concentrations (.5 and 1 molar) of glucose and fructose to water, rejected, however, equimolar solutions of sucrose. Preferences were much more marked, if the birds could use the colour of the fountain as a secondary cue (relative preference for .5 M glucose if both fluids were presented in identical fountains 67.8 ± 5.4% of total fluid intake, after repeated presentations of both fluids in fountains of different colours 86.8 ± 2.7%; data for .5 M fructose are 68.5 ± 6.6% and 88.4 ± 4.2%, respectively). Rejection of sucrose, too, was augmented by this colour cue (identical fountains: 32.1 ± 2.9% of total fluid intake, different coloured ones: 6.5 ± 1.6%). These findings suggest, that the observed preferences are rather learned than immediate responses. Direct observations of the behaviour of starlings to taste solutions lead to the same conclusion: They show distinct immediate responses to solutions of quinine, but not to solutions of sugars. Higher doses of sucrose cause heavy diarrhoea in starlings, which might be the reason for rejection of this sugar.

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Differences between Resident and Migratory Individuals of a South-West-German Blackbird Population *(Turdus merula)*

Hubert Schwabl

Blackbirds in south-west Germany are partial migrants. Recoveries of banded birds show, that one part of the population winters in the breeding area, while the other migrates to southern France or northern Spain. To distinguish the migratory individuals from the residents, a population was trapped and banded in winter. In February the proportion of unringed birds suddenly increased. The arrival of unringed birds was thought to represent the migratory population. The age-proportion of migratory blackbirds trapped at a banding-station in the Swiss Alps (Col de Bretolet) corresponded to the age compositions of resident and migrant birds in the study area in that many more juvenile than adults migrated.

The size of the testes was significantly ($p < 0.02$) higher in residents than in migrants when the latter arrived. Singing, occupying territories and first territorial fights between males had already began, before the migrants arrived in spring. Resident pairs seemed to begin to breed earlier than migratory pairs. In fall, when the migratory birds left the breeding area, testes size was minimal and there seemed to be no difference between migrant and resident birds.

Geographical distribution and moult of the Cuckoo *Cuculus canorus* in the Western Palaearctic and Ethiopian regions

D. C. Seel

Hitherto, the wintering area of *Cuculus canorus* emigrating from the Western Palaearctic has been only poorly described. Ringing results (Seel, 1977, Ibis 119: 309—322) demonstrate patterns of emigration from and immigration into the Western Palaearctic but give little guide to either the timing of the main events in its annual cycle or the distribution of the species when absent from this region.

The present study is based on museum skins collected over most of the Western Palaearctic and Ethiopian regions. Old birds migrate southward earlier than first-year birds. 'Wintering' occurs in December-February principally south of the equator and mostly south of 10°S. The primary moult takes places in the wintering area but some birds retain a few old primaries during the northward migration. Old birds also migrate northward earlier than young birds, and old males mostly do so in advance of old females, presumably to establish home ranges before the latter arrive. Despite being a brood parasite, an adaptation which would appear to afford unusual opportunities for breeding, *Cuculus canorus* may be unable to breed at the southern end of its range because of the energy demands of its chief moult.

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Self Immolation of Haflong Birds

Sudhin Sengupta

It has been reported for a long time that the people of Jatinga village (Haflong), Assam, capture hundreds of birds daily by attracting them through artificial light. To study this mystery a trip was made in October, 1977 to Haflong.

The Jatinga village is situated in the Barail hill range and encompasses an area of 2 sq. km.

Heavy rainfall only during the months of August to October in dark night was the most important factor necessary for the initiation of the bird movement towards the source of artificial light. With the appearance of rains and directional wind (south to north) birds of diverse species in large number started coming from the north towards the lighted area. Soon they started circling the place again and again when suddenly some of them dropped down into the ground. While other birds dashed straight into the Petromax. Birds arrived mostly between 1900 hrs. to 2200 hrs. and 0200 hrs. to 0400 hrs. of the day. After alighting on the ground these birds either remained huddled together or squatted motionless. In the present case 15 bird species were involved in self sacrifice to the lighted Petromax.

We failed to attract any bird in rainless clear night by using Petromax and in other places of the Barail hill range. Detail report on this mysterious behaviour of Haflong bird would be published in due course.

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The Technique of DNA × DNA Hybridization

Charles G. Sibley and Jon E. Ahlquist

The genetic material, deoxyribonucleic acid (DNA), is composed of four chemical subunits called nucleotides, which differ in the structure of their "bases", namely, Adenine (A), Thymine (T), Guanine (G) and Cytosine (C). The DNA molecule is a double-stranded helix of long chains of nucleotides in which the two strands are held together by chemical bonds between complementary pairs of bases; A pairs only with T, G pairs only with C. Genetic information is encoded in the sequence of the nucleotides.

The two strands of the double helix of DNA can be separated ("melted") by heating the DNA in solution to a temperature that will dissociate the chemical bonds holding the base pairs together. Upon cooling the complementary base pairs (A—T; G—C) re-associate and the double-stranded molecule reforms. This property is the basis of the DNA hybridization technique in which experimental conditions are established such that DNA's from two different species are mixed together, "melted" into the single-stranded condition, and allowed to form "hybrid" molecules as they re-associate. The hybrid molecules are then heated and the temperature required to "melt" them is determined and compared with the melting temperature of re-associated conspecific DNA. The difference is an index to the similarity of the nucleotide sequences of the two species and hence to their genetic similarity.

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Überleben von *Mitu mitu mitu* (Linnaeus, 1766)

Helmut Sick

1766 beschrieb Linné das Hokkohuhn *Crax mitu* auf Grund der Angaben von Georg Marcgrave, deutscher Mathematiker und Mediziner, Begleiter des Grafen Moritz von Nassau, der 1636 nach Pernambuco, Nordostbrasilien, kam. Über 300 Jahre wurde dieser große Waldvogel nicht mehr aus Nordostbrasilien gemeldet. Das Marcgrave'sche Stück schien ein aus Amazonien stammendes gefangenes Exemplar gewesen zu sein. Im Amazonasgebiet ist ein ähnlicher Hokko relativ häufig, von Spix 1825 als *Crax tuberosa* beschrieben.

1951 erhielt Olivério Pinto, der bekannte brasilianische Ornithologe, in Alagoas, südlicher Nachbarstaat von Pernambuco, einen frisch geschossenen Hokko durch einen einheimischen Jäger. Es war die Marcgrave'sche Art, einziges bisher in ein Museum (São Paulo) gelangtes Stück (Weibchen).

1977 war es mir als erstem Naturwissenschaftler nach Marcgrave vergönnt, diesen Hokko lebend zu studieren: ein Weibchen, von Pedro Nardelli in einem Kistenverschlag in Alagoas entdeckt und nach Rio gebracht. Dieses Exemplar enthüllt bisher zu wenig beachtete (Schnabelfarbe: Basis rot, Spitze weiß) und unbekannte (Aurikularbe-

reich nackt, nur Ohröffnung befiedert) Charaktere, die diesen Hokko von seinem geographischen Vertreter in Amazonien unterscheiden. Das Fehlen einer weißen Schwanzbinde, und zwar auch im frischen (nicht abgeriebenen) Gefieder, wird bestätigt.

Die Erhaltung des MARCGRAVE'schen Hokko in den letzten Waldresten Nordostbrasiliens müßte durch Züchtung in Gefangenschaft garantiert werden.

Museu Nacional, Rio de Janeiro, Brasilien.

Osmotic and Volume Regulation in Salt Adapted and Non Adapted Pekin Ducks During Salt Loading

CHRISTA SIMON-OPPERMANN, HAROLD T. HAMMEL, HANS DEUTSCH and ECKHART SIMON

Pekin ducks were raised in two groups: one with dry food and tap water, the other with dry food and NaCl solution (600 mosm. kg^{-1}) as drinking water. After 6 months the animals were submitted to experimental osmotic loads consisting of continuous i.v. infusions of 740 mosm. kg^{-1} NaCl solution. The load was increased stepwise by infusing 0.25, 0.45 and 0.65 ml. min^{-1} of the solution during 9 h. Secretion rate and osmolality of the nasal salt gland fluid were measured in 15 min periods. Plasma osmolality and electrolytes and the amount and osmolality of cloacal excretion were controlled. In the salt adapted ducks, salt gland secretion started immediately after the beginning of salt loading. Input and output of salt and water were exactly balanced, and plasma osmolality (328 mosm. kg^{-1}) did not change. Non adapted ducks could only balance the volume load but retained part of the salt load, and plasma osmolality rose from 297 to 346 mosm. kg^{-1} during loading. Salt gland activity of the adapted ducks did not always correlate with plasma osmolality indicating the involvement of volume factors, besides tonicity receptors, in salt gland control. Salt gland responses to removing and infusing blood and to adding dextrane solutions to i.v. salt loads indicate that changes of interstitial volume may influence salt gland activity.

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New natural hybrids *Alectoris rufa* × *Alectoris graeca* from Maritime Alps and related taxonomic considerations

SILVIO SPANÒ

The occurrence of natural hybrids *Alectoris rufa* x *Alectoris graeca* is reported from some localities of the Maritime Alps.

The density of records within the same localities (Roya Valley), their distribution in the space of 4 years, as well as the fact that specimens have been always taken from apparently homogeneous flocks, all seems to point out the existence of a stabilized small population.

The existence of such hybrid population in other regions of the Maritime Alps had been reported however, since the early decades of this Century and is paralleled by recent recording (Dragoev, 1974) of hybrid specimens of *Alectoris graeca* x *Alectoris chukar* on the Rhodope Mts (Bulgaria).

The taxonomic significance of hybridisation belts at the distribution limits of otherwise allopatric species of *Alectoris* is discussed.

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Ei, Gelege und Nest der Mittelmeer-Silbermöwe *(Larus argentatus michahellis)*

Gerhard Spitzer

Nach der von Szielasko (J. Orn. 53: 273—297, 1905) abgeleiteten Formel zur Beschreibung von Umrißkurven von Vogeleiern wurde ein Computer-Programm entwickelt, das die Berechnung von Volumen, Oberfläche, Schwerpunktlage und Rollradius aus der Länge der Polachse und Stellung und Durchmesser des größten Parallelkreises erlaubt.

Eier der Mittelmeer-Silbermöwe *(Larus argentatus michahellis)* wurden auf die Bedeutung der oft sehr auffallenden Formunterschiede selbst zwischen Eiern eines Geleges untersucht. Dabei zeigte sich, daß die Eier ihren Oberflächengrößen nach zwei Typen angehören, oberflächenkleinen (relative Oberfläche $r0 = 1{,}16 \pm 0{,}04$) und oberflächengroßen ($r0 = 1{,}58 \pm 0{,}07$), die alternierend auch in der Legefolge von einem Weibchen erzeugt werden können.

Die Häufigkeitsverteilung der beiden Eitypen zeigt Korrelationen zum Bedeckungsgrad der Neststandorte, an stärker gedeckten Standorten überwiegen oberflächenkleine Eier, an weniger gedeckten oberflächengroße, an stark exponierten sind dann wieder oberflächenkleine zu erwarten (langkreiselförmige „Lummeneier").

Eigenschaften der Gelege lassen sich durch Größen der Regressionen von Paarungen von Parametern der Eiform beschreiben. So zeigen die Steigungen verschiedener solcher Paarungen Korrelationen zu Parametern des Neststandortes.

Für homogene Gelege, die nur Eier eines Eityps enthalten, lassen sich keine Korrelationen der Brutdauer zu Eivolumen, Eioberfläche und Parametern des Neststandortes nachweisen, während für heterogene Gelege eine Beeinflussung der Brutdauer über divergierende Stellwerte der Eier unterschiedlichen Typs auf die Bruthandlung des brütenden Vogels nachzuweisen ist.

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Influence of Age of Mates on Reproduction in the Pied Flycatcher *Ficedula hypoleuca*

Helmut Sternberg

Based on recovery reports of 783 breeding pairs of *Ficedula hypoleuca*—both mates were ringed as nestlings—in the Eastern part of Lower Saxony (Federal Republic of Germany), exact data for egg-laying, clutch size, number of hatched and fledged young and recovery rates are available. The results are:

(1) In total, in 33% of all pairs males and females were of the same age. This rate is 28% above chance expectation.

(2) On average, pairs in which males or females were older than 3 years laid 2 days earlier than the 2 year-olds and 7 days earlier than the yearlings.

(3) Females, older than 3 years, laid 6.23 eggs. This is more than in 2 year-olds (5.97) and in yearlings (5.44).

(4) Pairs composed of yearlings had a low fledging rate of 4.59 young, less than those of yearling males (5.45), yearling females (5.01) and older ones (5.36).

(5) The recapture rate of the offspring was smaller in pairs of yearlings (15.8%) than in the more than 2 year-olds (21.5%).

(6) The productivity index (recovery x fledged young per brood) $\cdot$ 100^{-1}

was: Pairs composed of yearlings: 0.72; Pairs composed of 2 year-olds; Pairs composed of 3 year-olds: 1.60.

The value of the different age-combinations of mates in relation to population dynamics in Pied Flycatcher is discussed.

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Seasonal Breeding in Grouse

K-A Stokkan & P. J. Sharp[1])

A comparative study was made of seasonal breeding in male Willow Ptarmigan *(Lagopus lagopus lagopus)* and Red Grouse *(Lagopus lagopus scoticus.* The concentrations of gonadotrophins and testosterone in the blood were at their highest during the breeding season and at their lowest during the photorefractory period, in summer, when the testes were regressed.

Castration at any time of year, including the period of photorefractoriness resulted in an increase in LH secretion followed by a decline. Low concentrations of plasma gonadotrophins in photorefractory birds thus seem to be maintained by the negative feedback action of testicular hormones.

After photorefractory Red Grouse were castrated and transferred from a long to a short daily photoperiod, the level of LH increased more slowly than after photorefractory birds

were castrated and kept on a long daily photoperiod. In contrast, after photorefractory Willow Ptarmigan were castrated and transferred from a long to short daily photoperiod, the level of plasma LH remained depressed. It is believed that this depression was due to the negative feedback action of adrenal steroids.

These observations suggest that seasonal breeding in grouse is regulated by changes in the sensitivity of the neural component of the negative feedback mechanism. The sensitivity of this mechanism appears to be greater in photorefractory Willow Ptarmigan than in photorefractory Red Grouse.

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Developmental characteristics in flight of young blackbirds (*Turdus merula* L.)

Hans-Jürgen Stork

Young blackbirds leave their nest at an age of 13 days—incapable of flight but running and hopping as well as their parents. Development of flight capability has been studied in a flight room, where young blackbirds were trained to fly over distances of 4 m, 10 m and 14 m. Flight data could be obtained from slow motion pictures.

The development of some flight parameters (flapping frequency, maximum speed, starting acceleration, landing deceleration, Reynolds number, reduced frequency) is described. Flight conditions may be ratable.

The flight parameters are to compare with morphological data of the growing flight apparatus (flight feathers, tail, wing area, geometry of the wing, profile parameters, weight, loading of the wings). Both groupes of parameters show similar developmental curves with large growth rates during the first phase of flight development up to the age of 26 days. During this phase landing is the most restricting situation for the young, because landing deceleration by use of the small wings and the short tail is still insufficient.

Later the young blackbirds may controll all flight situations. Up to the age of 40 days we only can find small changes in the flight apparatus and in the parameters of short distance flights too. In this second phase ability to fly becomes improved for a better manoeuverability. A larger maximum speed may be reached if there is a way given for a longer acceleration.

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The Moult of the Guillemot *Uria a. aalge*

C. Swennen

In Guillemots kept in captivity from the chick stage onward the moulting pattern has been studied during 6 years, starting in 1972.

There are two moults in the 12-month cycle, one prior to and the other after the breeding-season. All feathers are renewed during the post-nuptial moult, which starts with feathers of head and flanks followed by a shedding of the primaries a week later. The post-nuptial moult last about 110 days. During the pre-nuptial moult, which ends with the feathers of head and neck, initially a larger but later a smaller part of the body-feathers are renewed with increasing age.

Older Guillemots wear the nuptial plumage for a longer period than younger ones. This extension is obtained by contracting the prenuptial moult and by delaying the post-nuptial moult. The progressively earlier acquisition of the nuptial plumage—each year with about 17 days—might indicate a strong selection pressure favouring the early possession of this plumage. The delay of the post-nuptial moult decreases with age, being 20 days between age 1 and 2, and in later years 16, 6 and 5 days respectively. This progressive decrease in decline suggests perhaps ecological disadvantages in post-nuptial moulting at a still later date without further important benefits.

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Local Dialects and Kin-selection in Songbirds

Laszlo J. Szijj

The general theory that birds sing in order to defend their territories is questioned in the present paper, as it is recognized that such a reasoning can not account for singing by non-territory holdmales. It is suggested instead, that the chief function of birdsongs is to:

a. reinforce a social bond between members of a 'neighbourhood cluster' utilizing frequent repetition of shared elements in their songs, a phenomenon known as the 'local dialect syndrome'.

b. asses their chances of settling in an area which is already occupied by a local neighbourhood cluster of males possessing a distinct dialect. Non-territory holding males accomplish this by noting the presence or absence of shared elements in their own repertoire relative to songs sung by a local group of males.

Many recent studies show that male territory holders react more intensely to songs not representing their own dialect, a non-territorial male can quickly establish his chances by eliciting initial responses with his own song.

Mis-matching of repertoires is therefore a measure of 'spatial distance' between the singer and the local cluster, the more the mismatching the more distant the origin of the singer. Since birds acquire the basic elements of their repertoire before they depart their place of birth, mis-matching is also a yardstick of the 'genetic distance' between singers, the more similar the songs, the more likely that an approaching male is genetically related to members of a local cluster. Local males, by reacting less to a closely matching song, will increase the chances that the singer will settle in the area and eventually become a member of a local cluster. The result is an evident case of kin-selection.

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Investigations on Plasticity in Reproductive Behaviour of Starlings *(Sturnus vulgaris)*

J. Tahon and M. Devisscher

Removal or addition of eggs or young have apparently no harmful effects on the behaviour of breeding starlings. However, a minimum of one egg is required for the continuation of egg laying, two eggs are needed to keep the birds incubating and one pullus is a sufficient stimulus for the parents to bring food to the nest. The maximum of accepted eggs in a complete clutch is limited by the number that the female is able to incubate. In large broods, only competition between youngs for food and heat is determinant for survival.

Additive nestlings, even if the total of youngs is greater than the number of eggs originally laid by the female, are accepted and can be normally raised until fledging.

Starling clutches are predetermined. Addition or removal of eggs do not modify the number of eggs to be laid.

Both substitution of recently laid eggs by already largely incubated ones and vice-versa, are easily accepted by the breeding birds. Furthermore, incubation of the clutch is even not at all biologically required. On the other hand, starlings provided at the end of incubation time with newly laid eggs are still able to incubate them successfully during a period of twelve days.

Hatching is not an event sharply limited in time. It lasts nearly two days between the beginning of hatching and the begging of food, with a progressive decrease of incubation instinct and an increase in feeding trends. Adaptations required by an artificial advancement or delay of this phase are easily performed by the starlings.

Likewise, a sudden advancement or regression in age, obtained by replacement of native youngs by nestlings coming from others broods are accepted without apparent shocks, though the parents are obliged to immediate adjustments of their behaviour concerning the type of food (large or little items), the technics of feeding (at the hole or inside the nest), the warming up of the youngs, etc.

Due to important requirements caused by a rapid growth, youngs survival in large broods is a simple question of competition between them for food and heat, especially during their first six days of life.

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Ethökologische und morphologische Differenzierung von Goldhähnchen (Regulidae) bei Nahrungssuche und Nahrungswahl

Ellen Thaler

Das Verhalten der in Mitteleuropa syntopisch vorkommenden Zwillingsarten Wintergoldhähnchen *(Regulus r. regulus)* und Sommergoldhähnchen *(Regulus i. ignicapillus)* bei Nahrungssuche und Nahrungswahl wird geschildert. Die Arten unterscheiden sich be-

sonders im Größenspektrum der Beutetiere. Dies erlaubt die Koexistenz bei sonst gleichartigen Ansprüchen an den Lebensraum auch in sich überdeckenden Revieren.

Beziehungen zwischen Nahrungssuche, Nahrungswahl und Schnabel- und Schädelproportionen werden erläutert.

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Plumage Succession of Nestling Maguari Storks

Betsy Trent Thomas

Nestling storks *Euxenura maguari* have two successive coats of down. At hatching the down is white; the second down is very dark gray. By 10 days the nestling has a starry appearance because white downs remain attached to some of the dark second generation downs. The first black juvenal feathers begin to emerge at 18 days. White feathers become clearly visible on the face by two months and at three months the juvenile bird resembles the adult color pattern.

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Adaptations of sandgrouse (Pterocliidae) to their thermal and osmotic environment

David H. Thomas

Sandgrouse are characteristically birds of arid and semi-arid Afro-Asia. They are small (250—500 g), diurnal, ground-living animals: thus, despite a relatively unfavourable surface/volume ratio for water and thermal balance, they spend most of their time in an air layer of temperature extremes (up to 55°C; 4h/day at > 50°C: Thomas & Robin, J. Zool., London **183,** 229—249, 1977) and most birds drink only once per day.

Environmental and metabolic heat loads are minimised by limiting vigorous activity to the cooler times of day, by remaining inactive when the sun is high, and by increasing thermal insulation when ambient temperatures exceed body temperatures.

Water is conserved by suppressing evaporative heat dispersal mechanisms until achievement of maximum insulation against environmental heat loads. Renal morphology suggests adaptation for water and salt retention. Morning drinking flight behaviour shows evidence of an anticipatory response enabling more individuals to drink earlier in advance of hotter conditions later.

In a recent study (Thomas & Robin, 1977) interspecific differences in breast feather water carrying characteristics and in renal morphology were found to reflect differences in ecological adaptation to arid environments.

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Pursuit Flights and Territorial Behaviour by North American Ducks of the Genus *Anas*

Rodger D. Titman

The objectives of this study were to compare and contrast two associated aggressive components of breeding behaviour in North American ducks of the genus *Anas*. It was hypothesized that pursuit flights are primarily responsible for spacing and territorial defence in this genus. Field studies of *Anas platyrhynchos*, *A. rubripes*, *A. americana*, *A. strepera*, *A. discors*, and *A. clypeata* strongly support this hypothesis. Other studies of *A. acuta* and *A. crecca carolinensis* have shown these species to disperse as a result of pursuit flights, but territories could not be defined for them (McKinney, 1975. In Baerends, Beer, and Manning. Function and Evolution in Behaviour. Oxford, pp. 331—357). However, the frequency of performance of pursuit flights and other aggressive displays, territory size, overlap of territorial boundaries, and duration of site attachment differ considerably from one species to another. Associated with pursuit flights frequencies of male-to-male aggression and male-to-female aggression, attempted rape, and successful expulsion of intruders from territories vary from species to species as well as the average duration and intensity of pursuit flights. Just the same, similarities in form and function of pursuit flights are apparent throughout the genus.

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Factors Influencing Emperor Penguin Mortality at Cape Crozier and Beaufort Island, Antarctica

Frank S. Todd

Emperor penguins *(Aptenodytes forsteri)* are winter nesters that typically breed on relatively flat annual ice. Chick mortality may be very high, but adult mortality is generally low. Since 1974, the rookery at Cape Crozier, Ross Island (77°25′ S., 167°50′ W.) has moved between the Ross Ice Shelf and the unstable rock cliffs of Cape Crozier. This move has resulted in substantial adult mortality caused by falling rock. The move may have been prompted by a preference for rookery site "stability", i.e., avoidance of premature sea ice breakout. The choice may be disastrous because while the species can tolerate high chick mortality, it may not be able to absorb high adult mortality, particularly in a small rookery (300—400 birds). Any benefits the present rookery location provides seem offset by the rock slide dangers. A major midwinter slide could wipe out the entire population. As long as penguins continue to seek the "security" of the current site, the rookery remains vulnerable.

The Beaufort Island rookery (76°56′ S., 67°03′ E.) is more typical and while chick mortality was high in 1976 (65—70%), adult mortality was insignificant. Emperor penguins are apparently able to absorb high breeding failure because of their presumed long reproductive life and relatively low adult mortality rate. The high incidence of adult mortality at Cape Crozier is atypical and localized.

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Two Sibling Species of *Tyrannus* (Fam. Tyrannidae)

Melvin A. Traylor Jr.

The Tropical Kingbird, *Tyrannus melancholicus*, ranges through tropical Central America north through eastern Mexico to southern Texas. The populations from Texas to central Veracruz have been recognized as the subspecies *couchii*, larger and paler than the Central American race. However, by use of two characters, the ratio bill length/wing length, and the wing tip index describing the relative length of the 10th and 5th primaries, it can shown that *couchii* is a distinct species, ranging from Texas through eastern Mexico to Yucatan and northern Guatemala. It is sympatric with *melancholicus* south of San Luis Potosi and southern Tamaulipas.

Couchii is primarily a bird of dry thorn scrub, while *melancholicus* is found in almost any habitat outside of wet forest. In northern Mexico and the Yucatan peninsula they occur in about equal numbers with no evidence of hybridization. However, in southern Veracruz, *couchii* is rare compared to *melancholicus*, and intermediate specimens are found that suggest hybridization. It is speculated that at one time the range of *couchii* was divided by the forest of the Isthmus of Tehuantepec, and that only recently has *couchii* reentered the area through man-made clearings. Because of the rarity of conspecifics, *couchii* breeds with *melancholicus* there.

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Orientation and Activity Behavior of Blackcaps

Wolfgang Viehmann

During autumn and spring migration 1975—1978 the non visual orientation and the "Zugunruhe" of Blackcaps *(Sylvia atricapilla)*, trapped in the Rhein-Main-Area were analysed.

a) Orientation. The tests showed that Blackcaps were able to get oriental information from the local geomagnetic field (0.46 Gauss, mN 360°, 66° Incl.). When the horizontal component (0.46 Gauss, mN 180°, 67° Incl.) or the horizontal and the vertical components of the Earth magnetic field were reversed (0.46 Gauss, mN 350°, −60° Incl.) the Blackcaps changed their directional Preferences according to these artificial magnetic fields. In a partly compensated magnetic field (0.34 Gauss, mN 360°, 60° Incl.) the birds were not able to orient.

The observed behavior indicates that Blackcaps use an inclinationscompass for orientation as it was described for European Robins (Wiltschko and Wiltschko. Science 176: 62—64, 1972). During spring migration the individual test birds showed directional preferences ca. 180° opposite to the corresponding directions in autumn. The headings of the individual birds suggest that a mixed population of SE and SW migrants was tested.

b) Zugunruhe: The registration of the activity showed that Blackcaps had three different patterns of Zugunruhe: 1. in the first part of the night, 2. in the second part of the night and 3. during the whole night.

A correlation of the Zugunruhe and the orientation of the individual birds indicates that the SW-migrants are mostly activ in the first part of the night and the SE-migrants have their Zugunruhe mostly in the second part of the night and during the whole night.

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Hunting Strategies of *Falco eleonorae* and *F. concolor*

Hartmut Walter

The density and height of bird migration across the Mediterranean Sea and the Arabian Gulf varies according to geographical, seasonal and climatic factors. Studies on breeding populations of Eleonora's Falcon *(Falco eleonorae)* in Mallorca, Crete, Cyprus and Morocco, and of the closely related Sooty Falcon *(F. concolor)* in Bahrain indicate that the falcons possess a considerable number of options regarding hunting technique, location and period. This enables them to respond to specific and frequently changing prey concentrations in their breeding locations in an optimal fashion.

Each breeding population uses a characteristic spectrum of hunting strategies which differs from those used at other breeding sites.

While Eleonora's Falcon hunts bird migrants only in the air above sea and immediate seashore areas, the Sooty Falcon pursues also non-migrating birds on the ground. The latter can be understood as an adaptation to an apparent low density of insectivorous passerine migrants flying across the Arabian Gulf during the height of the young falcon's growth period in late September/early October.

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Ecological guilds along the elevational gradient in the Swiss Alps

Beat Wartmann

The breeding birds of Swiss Alpine valleys have been grouped into foraging guilds. For each altitudinal belt of 200 m (c. 660 feet) the different proportions of species and individuals belonging to each guild are discussed. The relatively constant sum of the proportions of tree-dwelling and ground-dwelling individuals particulary illustrates the crucial importance of the habitat structure.

The elevational gradient influences the numbers of species and of individuals in different ways, depending on the particular guild. The results are discussed along the line of the following hypothesis: Compared to the ground-dwellers and the herbivorous tree-dwellers, the guild of the carnivorous tree-dwellers should contain a higher proportion of specialist species. These specialists should be affected more strongly by the general reduction of food resources with increasing altitude.

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Meliphaga Honeyeaters in Papua New Guinea: A report on the range and identification of the *Meliphaga analoga* group

Inez L. Weston

As a prerequisite to any study of the *Meliphaga* species it is essential to be able to accurately identify each species. Difficulties in identification in the field have resulted in observations usually being recorded simply as "*Meliphaga sp.*"; thus very little is known of breeding and nesting activity, behaviour and ecology, of four very similar species. A bird-in-the-hand identification key is presented for *M. albonotata, M. aruensis, M. analoga* and *M. gracilis,* based on over three years banding studies in southeastern Papua New Guinea. With experience, these keys can be applied to field observations, except possibly in the case of *M. analoga.* The range of each of these species throughout the Papuan sub-region is shown, including new altitudinal levels for *M. albonotata.* Brief notes on the history of *M. montana* and *M. albonotata* are included. A tabulation of weights and measurements is given and photographs of plumage characteristics are presented, together with photographs of four species of *Meliphaga* which have been mistnetted within a study area of less than 50 m square.

Port Moresby, Papua, New Guinea.

Biology of Peregrine Falcon in Victoria, Australia: One of the First Well Studied Populations in the Southern Hemisphere

Clayton M. White and Stephen G. Jones

This study was designed to determine: (1) population density, (2) reproductive success, (3) feeding habits of the peregrines in Victoria and to help develop a program to determine their movements by banding and marking. The possibility of chemical interferences with the breeding effort was investigated.

A total of 162 known or suspected eyries were documented in Victoria, an area of about 145,000 sq. Km. Of these nest sites, 95 were on cliffs, 10 in abandoned stone quarries, 26 in hollow trees, 21 in stick nests in trees, 7 in unidentified, and 3 in unspecified sites. An estimated one-third to one-half of the actual number of eyries in Victoria are known, hence between 300—350 pairs breed there.

We visited 100 nesting areas to measure productivity. The mean clutch size was 2.7 eggs. Young fledged from approximately 50% of the eyries checked for a fledging rate of 2.1 young per successful nest (one that fledged young) and 1.0 young per active area (adults present). A total of 92 young was banded in 1976 and 1977.

We recorded 65 bird species and 2 mammal species as prey of the peregrines. The three most important species were the Domestic Pigeon, Galah and Common Starling. Collectively, these species made up 51.8% of the food by numbers. Parrots made up 36.1% of the food by numbers, being recorded in over 90% of visited eyries.

DDT is used in excess of 4 lbs/acre/annum in some parts of Victoria and used generally at lower levels over many parts of the state. In 1976 seven eggs and in 1977, 26 eggs were

collected for hydrocarbon analysis. Regarding the seven samples from 1976, DDE contents varied from 5 to 24 ppm (wet wt.). Fifteen eggs between 1923 and 1952 had an eggshell "thickness index" of 1,962. Four eggs from 1968—69 had an index of 1,697, representing a 14% decrease. The combined 1975—76 index was 1,485, a 25% decrease. The thinnest eggshell, found crushed in the eyrie, had decreased in thickness about 30%.

Genetical Aspects of Dimorphism in Eleonora's Falcon *(Falco eleonorae)*

Michael Wink*), Dietrich Ristow**) and Coralie Wink*)

Dimorphism of *Falco eleonorae* was studied in a large Aegaean colony. Among the adult falcons the percentage of the dark phase is 33.5% (1977) and seems not to have changed significantly during the last 13 years (1965—1977). 31.6% (1977) of all fledglings belonged to the dark morph. The phases of the breeding pairs are distributed randomly. The heredity of dimorphism follows the Mendelian laws: the dark morph is dominant and the light is recessive. The homozygote dark phase is represented at 3.4%, the heterozygote at 30.1%, and the recessive light phase at 66.5%.

A similar difference of colours could also be observed in the eggs, clutches usually containing light and dark brown eggs. It could be shown, however, that this phenomenon was not correlated to the respective morphs of plumage, but to sequence of egg-laying: the first egg usually being light, the second and third egg dark.

The differences between light and dark phases of adult and juvenile falcons are demonstrated.

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Untersuchungen zur Stadtökologie in Berlin

Klaus Witt und Hinrich Elvers

Im Süden Berlins wurden 1976—1977 alle Brutvögel auf 25 Rasterflächen von ca. 1 km² Größe kartiert. Die Gesamtfläche ist ein Transsect vom Stadtrand mit Ödland und Neubauviertel über baumreiche Villenviertel mit eingestreuten Parks zur geschlossen bebauten City-zone. 59 Brutvogelarten wurden erfaßt, davon nur 21 mit einer Stetigkeit über 50%. Die 38 weniger stetigen Arten waren an kleinflächige Habitate wie z.B. Ödländereien und Parks gebunden. Die Artenzahl pro Rasterfläche erreichte in vielfältig strukturierten Gebieten (Stadtrand, Großpark) 36, im baumreichen Villengebieten 24—31 und sank mit zunehmender geschlossener Bauweise bis auf 8—9 in Altbauwohn- und City-viertel.

In 9 1965—1976 unter synökologischem Aspekt untersuchten Grünanlagen Berlins, die als integraler Bestandteil der Großstadtlandschaft anzusehen sind, brüteten 41 Vogelarten. 10 Arten kamen mit hoher Stetigkeit in allen Anlagen vor. Einige Arten wiesen charakteri-

stische Maxima (Abundanz und Dominanz) ihres Vorkommens in einem bestimmten Bereich des Hemerobiegradienten auf. Die Aufschlüsselung nach verschiedenen Nistweisen ergab ein Ansteigen der Höhlenbrüter vom Innenstadtbereich zu den Außenbezirksanlagen. Die Diversitätswerte nach Shannon-Weaver, berechnet numerisch für die Reviere und die gesamte Biomasse, stiegen zum Randbereich hin an, die Biomassewerte mit charakteristischen Minima in Probeflächen mit hohem Anteil schwergewichtiger Arten. Die Artenzahl stieg zum Randbereich hin ebenfalls an.

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Multiple Brooding in the Silver Gull *Larus novaehollandiae*

R. D. Wooller

The Silver Gull *Larus novaehollandiae* breeds at different times in the year around the Australian coast. In the east, south-east and south-west laying occurs in the spring and summer, in the north-west in autumn and winter, while in parts of the west both autumn and spring nesting occurs.

During 1977, Silver Gulls on Cornac Island, near Perth, Western Australia, laid eggs in all months from March through to November, with a major peak in autumn (April) and a smaller spring peak (August/September). The same individuals were present throughout the breeding period and many pairs laid several times (55 % twice, 18 % three times and 1 % four times). Most eggs laid were replacement clutches due to the heavy egg and chick losses. The apparent spring peak resulted from overlapping distributions of successive relaying attempts. Nest-site and mate fidelity were high, both within and between years.

Intraclutch egg variation, and seasonal changes in clutch and egg sizes followed the patterns common among gulls. Egg sizes in clutches laid by the same individual were very similar irrespective of the time of year.

Murdoch University, Perth, Western Australia.

Ecological-Zoogeographical Analyses of the Major Elements of the Birds of Georgia (the Main Complexes of Modern Biotopes)

Revaz G. Zhordania

At present Georgia (caucasus) registers about 201 major (settling and nesting migrant) species of birds, which from landscape-ecological viewpoint have been grouped in the following main complexes of modern biotopes: woodland bird (dendrophilous species), plain bird (campestral species), saxatile bird (saxo-rupestrine), hydrophilous bird (hydrophilus species) and anthropogenous bird (sinanthropous species).

From the abone mentioned major species of avifauna of Georgia there are 93 species of dendrophilus, where 19 species are faunal and 5 species dominant; 67 are campestrophilous species, among them 12 species are faunal and 5 dominant; 40 are saxorepestrine species, among which 7 are faunal and 1 is dominant; 39 are sinanthropous species, among which 15 are faunal and 4 dominant.

Besides these abone mentioned species there is a number of intracomplicant species. If we consides the species quantitavily out of 201 species 61 are ordinary and numerous, but 140 species are rare and few.

Tbilisi State University.

NACHTRÄGE, OHNE KURZFASSUNGEN
Addenda, without abstracts

Growth and Survival of Young White Ibis in Victoria, Australia

Sidney J. Cowling

Fisheries and Wildlife Division, P.O.B. 41, East Melbourne 3002, Australia

Dispersion Patterns of Wintering Blackbird and Starling Roosts in the Southeastern United States

M. I. Dyer

Colorado State University, Fort Collins, Colorado 80523, U.S.A.

Unilateral Memory Formation and Interhemispheric Communication in Day Old Chickens

Marie Gibbs

University of Sussex, Brighton, BN1 9QG, United Kingdom

Seabird Distribution in Winter in the North Sea

Claude Joiris

Vrije Universiteit Brussel, Pleinlaan 2, 1050 Brussel, Belgium

Foraging Efficiency and Roost Formation in *Quelea quelea*

S. Manikowski

Jaquiellonian University, Krupnicza 50, 30—060 Krakow, Poland

The Bird Collections of Merseyside County Museum

Peter Morgan

Merseyside County Museums, Liverpool, L3 8EN, United Kingdom

A Guide to the Birds of South America

C. C. Olrog

Instituto Miguel Lillo, Miguel Lillo 205, 4000 Tucuman, Argentinia

Comparative Biology and Ecology of Blackbrowed Albatross (*Diomedia melanophris*) and Greyheaded Albatross (*D. chrysostoma*) at South Georgia.

P. A. Prince and J. P. Croxall

British Antarctic Survey, Madingley Road, Cambridge, CB3 0ET, United Kingdom

Metabolism of Tropical Hummingbirds

Karl-L. Schuchmann

Fachbereich Zoologie, Siesmayerstraße 70, 6000 Frankfurt, Bundesrepublik Deutschland

Artificial Nest Sites of Imperial Eagle

Jàn Švehlik

Vojenskà 4, 04001 Košice, Czechoslovakia

Versuche zum Riechvermögen junger Gänse verschiedener Arten

Irene Würdinger

Pädagogische Hochschule, 3200 Hildesheim, Bundesrepublik Deutschland

FILME

FILMS

Die folgenden Kurzfassungen sind unverändert aus dem Filmprogramm übernommen. Auf die Angabe des Vorführdatums wurde verzichtet. Die Reihenfolge entspricht ungefähr der Darbietung.

BEHAVIOUR AND MONOGRAPHIES 1419
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BEHAVIOUR AND MONOGRAPHIES

Breeding Biology of *Pluvianus aegypticus*, the Egyptian Plover

T. R. Howell

Pluvianus buries its eggs in the sand where they are kept at appropriate temperatures by a combination of parental incubation, solar heat, and cooling by wetting. Young birds are also completely covered with sand by the parents when danger threatens. The film includes the following scenes: the nesting habitat (river sandbars); pair making nest scrapes, displaying, foraging by scratching turning stones; the buried eggs; nest attendance by parents, excavation and covering of eggs, soaking ventral feathers, wetting nest; newly-hatched chick emerging from sand; parents attending chick, covering it with sand as predator approaches.

The Private Life of the Herring Gull

M. Tibbles (BBC)

A round-the-year story of an island colony of gulls in the Bristol Channel. As we follow them through the seasons, we delve into some of the intricacies of their lives: their subtle posturings, their feeding in behaviour, and their mewing calls — so vitally meaningful to them, and to us an evocative reminder of seaside holidays.

The Private Life of Jackass Penguin

D. Fisher (BBC)

A close look at the "unknown" penguin — the least-studied of the world's eighteen species.

Jeffery Boswall lives with a million birds to try to unravel the intimate secrets of their life-cycle: their home-making and love-making, their territorial aggression and the problems of overheating when ashore.

The Private Life of the Wild Duck

M. Tibbles (BBC — Time Life Films)

The Mallard drake has a flashy but beautiful plumage which he uses to great advantage in his spring displays. The duck is more soberly dressed for the important task of

rearing her family of precious ducklings until they are ready to join the autumn flocks. In this film the full year's cycle in the life of the wild duck is revealed in all its intricate detail.

The Private Life of the Swan

M. Tibbles (BBC)

The Mute Swan is the largest and most graceful bird in Britain. This film gives a close-up view of its life-style following first the story of a pair of nesting swans — known to the local water bailiff as William and Mary—and then the story of their offspring until they in their turn start to breed.

Ocean Wanderers (Albatross)

(Austral. Broadcasting Comp.)

Albatross breed on only a few small windswept islands scattered about the Southern hemisphere. Macquarie Island is one of them. Each year about a dozen of the great Wandering Albatross come ashore to make a lonely nest on the tussocked slopes above Caroline Cove. They have only one chick and it sits out a full year in solitude, growing slowly on the food brought to it every few weeks through the long sub-antarctic winter.

Rearing young is an easier task for the Black Browed and Grey-headed Albatross. They can raise a chick in the summer and get it away before winter sets in.

The Flight of the Snow Geese

J. and D. Bartlett (Anglia Survival Ltd.)

Australian naturalist camera team, Des and Jen Bartlett, set out to cover, for the first time, the entire migration story of the 300 000 snow geese who nest on the tundra to the west of Hudson Bay and then journey south, 2,500 miles, to Texas and the Mississippi Delta.

The Bartletts were parents of some goslings. This film tells in full, not only the adventures of the clanging, clamouring packs of wild geese, but those of the orphans who eventually had to make the break with their human "parents" and find their way back into the wild.

Never Forget a Face (Bewick's Swan)

M. Tibbles and P. Fuller (Anglia Survival Ltd.)

Bewick's Swan is a small pure-white swan which migrates from Siberia to England every year, and one flock goes regularly to Slimbridge to swim on a lake outside Sir Peter Scott's window. Anglia Survival sent Maurice Tibbles to film the unique research at Slimbridge, where they follow the fortunes, not of the species as a whole, but of the individual characters, some of them eccentrics, who make up the flock. In the course of the work, the Wildfowl Trust's staff came up with disturbing evidence of hooliganism, which would have remained secret but for the silent witness of the swans they know by name.

The Prize Booby

B. Nelson (Anglia Survival Ltd.)

The boobies and gannets, the bird family Sulidae, are wideranging and successful, and unique in at least two respects. They fish as no other birds do, powerdiving from fifty feet into the sea; and in their behaviour to each other these powerful and aggressive birds have developed a code of behaviour designed to avoid fighting.

With the world's expert on the Sulidae, Bryan Nelson of Aberdeen University, Anglia Survival explores the world of the boobies and gannets from the Bass Rock to the Galapagos Islands.

Jackass City

D. and J. Bartlett (Anglia Survival Ltd.)

Des and Jen Bartlett set up their camp on the edge of this riotous boom town, to live with the penguins and to record their everyday life.

Here we met the bird itself, tough but not indestructible, battling with alien elements and hungry predators for the right to breed in its chosen site. Tender courtship alternates with fierce battles for lodgings in the windswept city. Underwater we see the penguin's speed and grace in its own element, contrasting sharply with its struggles on land, not only with the driven dust of the desert, but with persistant egg-thieves and baby-snatchers such as the Great Skua. Sealions wait offshore to snatch at the fringes of bathing parties.

The Year of the Kings (King Penguins)

(Austral. Broadcasting Comm.)

Each year tens of thousands of King Penguins gather to breed on the beach at Lusitania Bay, Macquarie Island. In depicting the activities of the full cycle of the year the film describes the social organisation of the colony and shows the King Penguin's finely balanced adaptation to the harsh environment. It also includes illuminating

sequences on the penguin's predators—the skuas and the feral cats—and a study of the graceful light mantled albatross nesting in and in flight from the hills that dominate the massive beach colony at Lusitania Bay.

Arctic Summer (Snow Geese)

D. and J. Bartlett (Anglia Survival Ltd.)

The Artic spring and summer on the tundra around Hudson Bay are short, perhaps barely two months long. In that time, all birds that converge on this lonely place from as far south as South America and the Antarctic ice cap have to find nesting sites, settle down and raise their families. This film looks at their intimate lives in the early part of that struggle against time and the elements.

Devil Birds

T. Allen and P. Bromhall

"Devil Birds" is on the Swift, *Apus apus*, and was filmed in the Oxford University Museum Tower where David Lack did his studies on this species. The film was taken by Tony Allen and Darek Bromhall.

Central Flyway (Snow Geese)

J. and D. Bartlett (Anglia Survival Ltd.)

Here Des and Jen Bartlett follow the geese down the Central Flyway of America, stopping off to capture rare nuggets of wildlife film such as the fantastic booming display of the prairie chickens in Texas and the even crazier mating antics of the Western Grebes who run upright on the water in courtship.

Behaviour of the Whale-headed Stork

W. Möller

Breeding behaviour: The Film shows the greeting ceremonies at the nest, the bringing in of nest material, the incubating and cooling of eggs as well as feeding the chicken at various ages.

Feeding Behaviour: In Uganda the food of the Whale-headed Stork seems to be mainly lungfish (up to 80 cm length). The hunting method is heronlike: long time waiting or calm careful striding with sudden attacks on the prey.

Big Bill—The Story of a Heron

(RSPB)

The patient killer, standing motionless for hours on end, the familiar figure of our waterways. When the heron does move into action—it does so with remarkable speed and a skill that makes it Europe's angling champion. We follow the life of one such bird we called Bill, watching him grow and seeing how he uses his big bill in the relentless search for trout, eels and goldfish.

Biologie des Waldrapp (Bald Ibis)

U. Hirsch

Twenty years ago two colonies of the Bald Ibis were found in Birecik. One was situated on the cliffs north-west of the village where the birds used to nest below the old castle walls. The remaining breeding colony of Birecik is situated in the centre of the town, at a distance of 300—400 m from the Euphrate river on a ledge in the upper third of a low sandstone cliff no more than 20 m high.

Financial support from WWF enabled the originator to observe and protect the colony throughout the breeding season in 1973 and to start a comprehensive education program.

The Vanishing Coveys (Partridge)

C. Knights and T. Anrewartha (Anglia Survival Ltd.)

This is the negative side of the story that the cameras of East Anglian naturalist camera team, Chris Knights and Terry Anrewartha, have to tell. But there is a positive aspect, too, and not least in the life of the partridge itself. Large coveys of partridges were once as much part of the British country-side as the elm and the hawthorn hedge. Recently, like both of these, they have been steadily disappearing. The passing of the partridge has been mourned from many points of view.

Jungle Fowl in India and Ceylon

N. E. and E. C. Collias

This film shows the Red Jungle Fowl *(Gallus gallus)* in typical habit in sal *(Shorea robusta)* forest of the Siwalik Hills in north central India. This species breeds in the dry season when fires set by man are common as they have been for centuries. Illustrated are methods of study in the field, food habits, reproductive behaviour and some of the natural enemies of the Red Jungle Fowl. Also shown are the Grey Jungle Fowl (*Gallus*

sonnerati) in its natural habitat in northwest India and the Ceylon Jungle Fowl (*Gallus lafayetti*) in the Wilpattu National Park of Ceylon. Comparisons are made between the habitat relations of these two species and those of the Red Jungle Fowl.

The Red Jungle Fowl in Thailand

N. E. Collias

This film shows the Red Jungle Fowl (*Gallus gallus*) in its natural habitat of secondary forest and bamboo groves in west central Thailand. Emphasis is placed on its history as the wild ancestor of domestic fowl. Some of the early reasons for domestication within its original geographic range are illustrated, including the ancient and popular sport of game cock fighting, the use as decoys to aid in hunting of wild fowl, and as a source of food by villagers in the jungle.

The Gannets of Bonaventure

J. R. Murray (CBC)

Bonaventure Island in Quebec's Gaspe region is home to North America's largest breeding colony of Gannets. The continued existence and health of the colony is now threatened by pollution of the waters of the St. Lawrence Gulf.

Other birds which either nest here or visits include the Razorbill, the Nashville Warbler, the Marsh Hawk, the White-throated Sparrow, and three species of gulls.

The Public Life of the Street Pigeon

M. Tibbles (BBC)

A flock of street pigeons is not a chance collection of odd coloured gutter snipes but of birds wonderful suited to survive as our urban partners. This has enabled them to become probably the most successful birds in the world.

Reproductive Behaviour of the Ring Dove

W. Heinrich (IWF)

Since the Ring Dove (*Streptopelia risoria*) proved to be an excellent laboratory animal as well as a convenient object for ethological courses, a film was produced showing the biology of this bird with emphasis on the characteristic behaviour patterns of courtship, incubation, and brooding. There is no external sex difference; therefore the male in the film is marked with blue colour.

The Private Life of the Cuckoo

M. Tibbles (BBC—Time Life)

This film tells the story of a pair of Cuckoos that conduct their cuckolding in a colony of Reed Warblers. The hen lays twelve eggs each in the nest of a foster-parent. The young squatter cockoo on hatching, evicts the warbler eggs or chicks and takes for itself all the food the nanny warbler can collect. When the juvenile cockoo is full grown it completely dwarfs the warblers but they continue to feed it until it flies off.

Ziegenmelker (Nightjars)

G. Wustig

Im Film wird der Ablauf einer Schachtelbrut gezeigt. Das Männchen versorgt vom 12. Tag an allein die Jungen der ersten Brut mit Nahrung. Zu diesem Zeitpunkt hat das Weibchen bereits an einer anderen Stelle ein zweites vollständiges Gelege.

Außerdem wird gezeigt, wie der Ziegenmelker in Lethargie gebracht wird.

Inside Story (Blue Tit)

S. Morris and D. Thompson (Anglia Survival Ltd.)

What happens during courtship, nesting and incubation of the Blue Tit? This bird is a hole-nester, sometimes using hollow trees but often nesting in nest-boxes provided for it. Oxford Scientific Films' camera techniques have managed to pry inside a nest-box, following every intimate phase of a pair of blue tits' struggle to raise their family.

The Private Life of the Starling

R. and R. Eastman (BBC)

The Starling is the commonest and most successful bird in the world. Why is it so numerous? Is it the farmer's friend or foe? Why does it spray its feathers with formic acid? Why does it commute to big cities for the night? What is the purpose of its "sun-set spectacular" when three million birds give the most impressive exhibition of aerobatics that can be seen in the whole world of birds?

Ural Owl

J. Švehlik

The film is about breeding of the Ural Owl in Slovakia with special point of view to its attacks to man near nest.

Schleiereule (Barn Owl)

G. Wustig

Der Film zeigt die nächtliche Jagd der Schleiereule auf Kleinsäuger (vorwiegend Feldmäuse). Die Aufzucht einer Brut (Spätbrut mit 8 Jungen) bis zum Flüggewerden und dem endgültigen Verlassen der Scheune. Bei der Untersuchung von Eulengewöllen werden Schädel von Feldmaus, Spitzmaus und Mauswiesel sichtbar.

In the Shadow of the Falcon

C. Aldridge (BBC)

This story is about the handful of wardens—men like Roy Dennis of the Royal Society for the Protection of Birds—who watch over rare, specially protected birds like the Peregrine Falcon and ensure that they can breed in peace undisturbed by egg collectors or illegal takers of the falcon's young.

Les oiseaux d'éléonore

M. Terasse

La plupart des espèces animales réellement menacées de disparition en Europe, sont soit exclusivement méditerranéennes, que ce soit l'aigle impérial d'Espagne, l'erismature, le goêland d'Audouin, la chèvre sauvage de Crête ou le phoque moine, soit des espèces à plus vaste répartition géographique, dont les populations méditerranéennes sont sur le point de s'éteindre comme le balbuzard pêcheur, le pygargue à queue blanche ou les grands vautours (fauves, moines et gypaètes).

Ces animaux pourchassés et cette nature à bout de souffle existent pourtant encore dans quelques paradis souvent cachés, mais toujours menacés.

Le film que nous avons réalisé est dédié à ces survivants qui ont trouvé sur quelques coins encore privilégées, leur ultime refuge.

Sous les ailes du condor

M. Terasse

De nombreux canards, des mouettes, des ibis souvent très proches des espèces européennes voisinnent dans la roselière avec le kamichi.

Ce film s'attarde à la recherche des nombreux canards et bernaches. Parmi ceux-ci, la très rare merganette des torrents, s'est adaptée aux cours d'eau les plus impétueux. L'un des rapaces les plus communs dans ces montagnes est l'aigle gris prédateur et rongeurs. Cette promenade a surtout pour but la recherche du condor des Andes.

Le bal des charognards

M. Terasse

Dans les Pyrénées à la fin de l'hiver, les Vautours et les autres charognards qui ont commencé à se reproduire connaissent les moments les plus difficiles.

Ils sont tous là, les corneilles et les grands corbeaux premiers arrivants et véritables indicateurs de la charogne, les milans royaux parasitent les autres convives, les vautours percnoptères et fauves, l'aigle royal, et couronnant ce prodigieux édifice biologique les gypaètes attendent calmement que le charnier enfin libre leur laisse encore l'opportunité de s'y nourrir d'os.

BIRDS AND THEIR HABITAT

Ellesmere Island

N. Archibald, J. Murray and R. Kovanic (CBC)

Ellesmere Island is on top of the world in Canada's High Arctic. Nesting ground of thousands of Arctic birds. It is home to wolves, caribou, muskoxen, jaegers, peregrine falcons and a myriad of delicate and beautiful arctic plants.

The Funks

N. Archibald and R. Kovanic (CBC)

Funk Island is a bleak chunk of granite, forty miles out from east Newfoundland. Most of the birds are Atlantic Murres, although there are a few puffins, razorbilled auks, kittiwakes and fulmars.

The Fisherman's Canaries

A. and E. Bomford (Anglia Survival Ltd.)

As sea pollution creeps round the coast of the world, even the remote Shetland Isles begin to suffer. But the Noup of Noss is still the biggest seabird colony in Europe, an amazing collection of puffins, guillemots, razorbills, and shags—and of course, gannets, master divers. Tony and Liz Bomford have photographed the birds at the height of the breeding season, looking in particular at their flight, above and below the sea surface.

The Arctic Islands—A Matter of Time

N. Archibald and R. Kovanic (CBC)

High Arctic is endangered as biological habitat unless the federal government acts now to form a policy and legislation similiar to that enacted by the ten provincial governments.

The film captures the spectacular beauty and unique wildlife of the Arctic.

Fish or Fowl (Barnacle Goose—Arctic)

C. Knights and T. Anrewartha (Anglia Survival Ltd.)

The film follows a flock of the Barnacle Goose three thousand miles on their round trip to breed in the uninhabited Arctic. In the north, some of them fall victim to predatory gulls, but during the short summer season, food is plentiful. When they fly south to escape the arctic winter, the entire Spitzbergen flock settles at Caerlaverock on the Solway Firth, where increasing shooting pressure once brought them nearly to extinction. Although there are Barnacle flocks elsewhere in the British Isles and Europe, they never mix with the Solway flock, and for a time it looked as if Spitzbergen would lose its Barnacles for ever.

Waddenzee

(BBC)

Where there's mud, there's wealth if you're an eider duck or avocet.

The "wealth" is the hoard of plants and tiny creatures that live within the mud, and are food for their bigger neighbours. How do worms that build snares of sand, blizzards of probing avocets, and the technology of fishermen make the rich economy work?

The Lonely Level

(RSPB)

This successful film is about the twenty-mile green ribbon of meadowland stretching through the heart of the Fens which is known as the Ouse Washes. In winter it is a vast flood prevention reservoir, one of the most important areas for wildfowl in Britain. In summer it is a flat expanse of meadows, dykes and pools, the vital British breeding ground for black-tailed godwits and ruffs. Sequences on these and other fenland birds were filmed against a background of local washland activities.

Bellamy on Heathland

(BBC)

David Bellamy, famous TV personality and expert on heathland ecology, takes us on a walk over this very important countryside. It is the home of a closely-knit community of living things and David shows us how these unique creatures have adapted to life on this specialised habitat, a habitat which is now the most threatened in Britain.

The Woodland Web

(BBC)

From earthworms burrowing their way through the soil, to rooks nesting up in the treetops. Woodland provides the most diverse range of habitats in the world. Plants, animals and birds living in the wood are all dependent on one another for food or propagation and the film examines the intricate relationships of this web of wildlife.

Extinction

(BBC)

In New Zealand there was once the oddest and most remarkable collection of birds in the world. Now the New Zealand Wildlife Service is trying to save those that are left.

This film is about the problems they face, how they are tackling them, and how they are discovering strange new facts about the last of those curious birds.

Wilderness Is Not a Place

A. MacGregor (RSPB)

The film features hauntingly evocative shots of estuaries in England and France. Its strong plea for estuaries cannot fail to strike a chord with anyone sympathetic to the conservation of wildlife and wild places.

Falken zwischen Island und Mauritius

R. Lammers

Verschiedene geographische Räume und darin beheimatete Falkenarten werden in diesem Film vorgestellt:

Island: Gerfalk (*Falco gyrfalco*) und Merlin (*Falco columbarius*); Mitteleuropa: Turmfalk (*Falco tinnunculus*) und Baumfalk (*Falco subbuteo*); Mittelmeer: Eleonorenfalke (*Falco eleonorae*); Mauritius: Der seltenste Falke der Welt, der Mauritiusfalke (*Falco punctatus*).

Afrikanische Adler in ihrem Lebensraum

R. Lammers

Vier charakteristische Adlerarten werden in ihrem Lebensraum vorgestellt:
Gaukler (*Terathopius ecaudatus*); Kampfadler (*Polemaetus bellicosus*); Habichtadler (*Hieraaetus fasciatus spilogaste*); Kaffernadler (*Aquila verreauxii*).

The Pampas

D. Fisher (BBC)

The expedition lives among the animals of the vast Argentine pampas. Here is the national bird, the hornero, with its mud open nest; also the snail kite complete with winkle-picker bill, and the grand archaic ostrich of South America, called the rhea. A night sortie reveals opossums and skunks, owls and armadillos.

Tierra del Fuego

D. Fisher (BBC)

The expedition reaches the Land of Fire at the southernmost tip of South America, a place of wild and rugged beauty. The Andean torrent duck—thought to be extinct—is filmed at home in the boiling tumult of a waterfall. You can join a voyage to uninhabited Staten Island, near Cape Horn, where no previous ornithologists have ever camped, and visit a millions-strong Rockhopper penguins colony where sea-lions prey with deadly efficiency on the penguins.

Through the Mangrove Marismas

D. Fisher (BBC)

A water-safari down the estuary of the Rio San Cristobal to the Pacific, through the hot, steamy and near-impenetrable jungle in search of strange animals and even stranger plants.

The Sea of Cortez

D. Fisher

Rasa Island houses one of the world's most impressive sea-bird cities: it's the headquarters of the rare and graceful Heermans Gull. The complex food chains are fascinatingly unravelled: we see the falcon that killed the gull that ate the lizard, that caught the fly that fed off the fish caught by the skill of the osprey.

Aladdin's Garden (Trinidad)

S. Morris (Oxford Scientif. Films)

When Oxford Scientific Films visited Trinidad, they were drawn at once to the Aripo Valley, where Rapse's garden sparkles among the mountains.

Cameraman Sean Morris filmed the glory of the flowers, and the dazzling beauty of the hummingbirds which find them the perfect source of food. Using a special high-speed camera, he reveals the extraordinary flexibility of their wings which enables them to hover and even fly backwards.

Do Not Disturb (Seychelles)

G. Edwards and P. Fuller

The Survival cameras take us to the Seychelles to see the rare life there. If birds like the Seychelles Bush Warbler or the Fody lost their homes here, the world would lose two more species. Many rare species of tern breed here, safe from egg collectors and hawksbill and green turtles that have been hunted almost to extinction find sanctuary.

Rottnest Winter

T. Riggert (ABC)

Each year the rains of April end the long dry summer of Rottnest Island, twenty kilometres west of Perth in the Indian Ocean. They bring an apparently brown and dead island to life again, and set off the breeding cycle of the Australian Shelducks which live on the salt lakes of Rottnest, but nest and hatch their young in coastal caves at the western end of the island.

Ascension Island

M. Tibbles (BBC)

Take a tiny island in the South Atlantic with forty volcanoes on it. Next, turn it into a ship by putting a garrison of Royal Marines on board. Make farmers of them and

send for plants and trees from all over the world. Let loose rats, cats, and donkeys; organise consignments of barn owls and mynah birds.

That's Ascension Island.

Graveyard Point (Patagonia)

D. and J. Bartlett (Anglia Survival Ltd.)

Graveyard Point in Patagonia, where on a tongue of desert reaching out into the Roaring Forties a wild mixture of Gulls, Cormorants and Skuas scramble to breed in the unfamiliar land environment.

Des and Jen Bartlett took their cameras to the Point, to film the chaotic conditions in a society composed entirely of rampart individualists: and they found to their surprise that under the riotous surface there's a strange kind of law and order.

LOCOMOTION

Bolzenflug

M. J. Csicsàky

Es werden Flugaufnahmen von weißen Zebrafinken zu sehen sein, die mit 200 B/s aufgenommen wurden. Wegen der Benutzung eines Umlenkspiegels sieht man die Rükken- und Seitenansicht des Vogels gleichzeitig und kann daher den typischen Flügelschluß der Bolzenflugphase gut beobachten.

Die Flugbewegungen rüttelnder Vögel

H. Oehme

Der Bewegungsablauf im Standschweben wird von Haustaube, Lachmöve und Dohle gezeigt. Die originale Aufnahmegeschwindigkeit betrug 104,5 B/s; bei einer Vorführgeschwindigkeit von 24 B/s entspricht das einer 4,35-fachen Zeitdehnung.

Wings Over the Rift (Gliding and Soaring)

J. Pearson (Anglia Survival Ltd.)

Television has recently bought a high performance sailplane, equipped with a tiny engine, for Colin Pennycuick, gliding expert and leading authority on bird flight, so that he may fly with vultures over the plains of Serengeti and the Rift Valley's lakes and mountains.

Flight

(BBC)

See the original magic carpet. Gasp for breath with jumbo swans straining to lift off. Thrill to the beauty and grace of the gliding albatross.

Vogelflug

G. Rüppell

Eine Übersicht über die wichtigsten Flugerscheinungen der Vögel: Segeln, Schlagflug, Landen, Starten und andere Manöver.

Vögel unter Wasser

W. Urban

Zwergtaucher, Haubentaucher, Bläßhuhn, Teichhuhn, Schwan und Enten werden bei ihren Bewegungen unter Wasser gezeigt. Außerdem enthält der Film Aufnahmen vom Stoßtauchen des Eisvogels.

MIGRATION

Flight for Survival

(RSPB)

The Arctic Tern for instance travels a round trip of 22 thousand miles each year. One of our swallows travelled 1 ¼ million miles in its lifetime, each year moving right down to South Africa to winter. The Sanderling travels from South Africa to breed in Greenland, stopping in Britain on the way. The film follows these birds and shows how we know what they are doing. It also covers the migration of several other birds.

Flyway

R. and R. Eastman (Anglia Survival Ltd.)

Each autumn millions of wild ducks, geese, and other birds migrate southwards through the United States to their winter quarters. This film follows them to the Mexico border. One of the rarest birds of all, the Whooping Crane, is also shown.

Migration
(BBC)

The magical mystery tours of many animals span the globe. Swallows fly a distance equivalent to the moon and back during their lifetime, and they will return to the same nest site year after year. What are the advantages of such a flight?

What kind of navigational clues do inter-continental travellers use?

Tony Soper follows our swallows south to see where they spend the winter.

SPECIAL BEHAVIOUR

Singing Songbirds
E. Arendt and H. Schweiger

The following species are shown: the European Starling (*Sturnus vulgaris*), the Grasshopper Warbler (*Locustella naevia*), the Chiffchaff (*Phylloscopus collybita*), the Willow Warbler (*Ph. trochilus*), the Winter Wren (*Troglodytes troglodytes*), the Nightingale (*Luscinia megarhynchos*) and the Red-spotted Bluethroat (*Luscinia svecica svecica*).

Competition for Food in European Vultures
C. König

The carrion-eating vultures may be classified into three feeding-types: 1. pecking species (*Neophron percnopterus*); 2. tearing species (*Aegypius monachus*); 3. pulling species (*Gyps fulvus*). Some sequences in the film show the different ways of feeding. But, these three ways of feeding overlap, so that competition still exists. It arises also with scavenging mammals, as dogs, foxes, etc.

Podiceps cristatus — Transport und Führen der Jungen
P. P. A. M. Kop

The young are carried on their parent's back where they get the protection and warmth needed. The bare skin patches on the head of the chick function as visual signals: the crown patch changes from grey to red for appeasement, the face-patches become red when the chick is satiated. The film shows a brooding bird on its nest, the behaviour of young climbing on their parent's back, and the transport of young and food-offering.

Podiceps cristatus—Courtship Behaviour

P. P. A. M. Kop

The courtship ceremonies include the Discovery Ceremony, the Retreat Ceremony, and the Weed-trick Ceremony. The Head-shaking Ceremony includes three types of which Type-2 is spontaneously performed and therefore true courtship, whereas two other types are common after agonistic encounters and serve as mutual appeasement behaviour to maintain the pair-bond. The types are distinguished by posture and different position of head-ornaments.

Bienenfresser und Blauracke — europäische Vögel im tropischen Gewand

W. Urban

Der Film zeigt das Brutverhalten des Bienenfressers mit einem Blick in die Nisthöhle. Nahrungsflüge werden vorgestellt. Der kürzere Teil über die Blauracke bringt ebenfalls Einstellungen vom Nest.

The Cry of the Gull

G. Montero and D. Fulton

A disturbing film about chemical pollution in Lake Ontario where toxic industrial wastes, like mercury, PCB and mirex, are causing serious reproduction problems in herring gull colonies.

The film shows an endangered gull colony on Scotch Bonnet Island on Lake Ontario where reproduction has dropped to one-tenth of that in normal colonies. Here, wildlife scientists have noted major changes in gull behaviour.

Fortpflanzungsbiologie der Zwergseeschwalbe

H. Rittinghaus

Kopulation, Nestgründung, Eiablage, Hudern und Füttern der Jungen werden gezeigt. Ein Beispiel für die Entstehung eines Hochschulunterrichtsfilmes aus der Encyclopaedia Cinematographica.

HISTORICAL FILMS

Balz und Kopulation von *Ptilonorhynchus violaceus* (Laubenvogel)

H. Sielmann

Abstract not received

Füttern kleiner Jungvögel beim Schwarzspecht (*Dryocopus martius*)

H. Sielmann

Abstract not received

Ethologie der Graugans

K. Lorenz

Abstract not received

PERSONAL FILMS

Roger Tory Peterson—Portrait of a Birdwatcher

J. R. Murray (CBC)

Here is chronicled the life of this extraordinary man in an hour film which includes some of Roger's own spectacular footage from Africa and the Antarctic.

TECHNIQUES

Methoden und Möglichkeiten des wissenschaftlichen Filmes

D. Haarhaus (WF)

Different methods from slow motion to x-ray film are illustrated by examples. Everybody who has a problem with filmwork should get an answer in this presentation.

Programm-Übersicht für Montag, 5. Juni, Monday, Program overview

Rooms:	A	B	C	D	E	F	G	H	I
10.00–12.30	Opening Session — Plenary *Lorenz* Oskar Heinroth								
12.30–14.00	Mittagspause / break for lunch								
14.00–14.30		Tafel-vorträge Poster Sessions							
14.30–18.30 incl. 30 min break	Filme films		Symp. 36 *Keast* Habitat	Symp. 2 *Nachtigall* Flight	Symp. 15 *Nottebohm* Birdsong	Symp. 9 *Gwinner* Circadian rhythms	Group 11 *Morgan* Historical collections	Group 19 *Sauer* Ratites	
18.30–20.00	Pause / break								
20.00	Filme films		International Bird Ringing Committee	Standing Committee Seabirds	Symp. 38 *Todt* Birdsong	Standing Committee Nomen-clature			(first PEC)

Programm-Übersicht für Dienstag, 6. Juni, Tuesday, Program overview

Rooms:	A	B	C	D	E	F	G	H	I
7.00– 8.30	Führung durch die Vogelsammlung im Zoo (Einzelheiten siehe Seite 17) Guided tour of the bird collections of the Zoo (for details see page 16)								
7.45– 8.45	Ornithologischer Spaziergang durch den Tiergarten (Einzelheiten siehe Seite 17) Ornithological walk through the "Tiergarten" (for details see page 16)								
9.00–10.00	Plenary *Aschoff* Biol. clocks								
10.00–10.30	Kaffeepause / coffee break								
10.30–12.30	Filme films		Symp. 37 *Peakall* Pesticides	Symp. 11 *Snow* Biorhythms	Symp. 17 *Thielcke* Vocal-ization	Symp. 1 *Feduccia* Pale-ontology	Group 9 *Karr* Numbering		
12.30–14.00	Mittagspause / break for lunch								
14.00–14.30		Tafel-vorträge Poster Sessions							
14.30–18.30 incl. 30 min break	Filme films		Symp. 19 *Sibley* System-atics	Symp. 16 *Ilyichev* Hearing	Symp. 10 *Berthold* Annual rhythms	Symp. 25 *Balda* Altruism	Group 1 *Oehme* Bird flight	Group 18 *Murphy* Raptor conserv.	
18.30–20.00	Pause / break								
20.00	Filme films		(first IOC)						

Programm-Übersicht für Mittwoch, 7. Juni, Wednesday, Program overview

Rooms:	A	B	C	D	E	F	G	H	I
7.00– 8.30	Führung durch die Vogelsammlung im Zoo (Einzelheiten siehe Seite 17) Guided tour of the bird collections of the Zoo (for details see page 16)								
7.45– 8.45	Ornithologischer Spaziergang durch den Tiergarten (Einzelheiten siehe Seite 17) Ornithological walk through the "Tiergarten" (for details see page 16)								
9.00–10.00	Plenary *Farner* Annual cycle								
10.00–10.30	Kaffeepause / coffee break								
10.30–12.30	Filme films		Symp. 22 *Hickey* Con-servation	Symp. 18 *Schwartz-kopff* Auditory system	Symp. 7/8 *Oksche* Endo-crinology	Symp. 26 *Immelmann* Imprinting			
12.30–14.00	Mittagspause / break for lunch								
14.00–14.30		Tafel-vorträge Poster Sessions							
14.30–18.30 incl. 30 min break	Filme films		Symp. 30 *Newton* Com-petition	Symp. 18 – con-tinued –	Symp. 7/8 – con-tinued –	Symp. 5 *Skadhauge* Osmo-regulation	Group 20a *Bock* Classifi-cation	Group 16 *Walter* Sylviinae	Group 2 *Balda* Social behavior
18.30–20.00	Pause / break								
20.00	Filme films		Inter-national Bird Ringing Committee	Group 15 *Schwartz-kopff* Bio-acoustics			Group 12 *Hickey* Con-servation		(second PEC)

Programm-Übersicht für Freitag, 9. Juni, Friday, Program overview

Rooms:	A	B	C	D	E	F	G	H	I
7.00– 8.30	Führung durch die Vogelsammlung im Zoo (Einzelheiten siehe Seite 17) Guided tour of the bird collections of the Zoo (for details see page 16)								
7.45– 8.45	Ornithologischer Spaziergang durch den Tiergarten (Einzelheiten siehe Seite 17) Ornithological walk through the "Tiergarten" (for details see page 16)								
9.00–10.00	Plenary *Keeton* Orientation								
10.00–10.30	Kaffeepause / coffee break								
10.30–12.30	Filme films		Symp. 12 *Schmidt-Koenig* Orientation	Symp. 21 *Luniak* Urbanization	Symp. 28 *Snow* Co-evolution	Symp. 23 *Krebs* Flocks	Group 14 *Follett* Endocrinology	Group 22 *van Bocxstaele* Congo-peacock	
12.30–14.00	Mittagspause / break for lunch								
14.00–14.30		Tafelvorträge Poster Sessions							
14.30–18.30 incl. 30 min break	Filme films		Symp. 12 – continued –	Symp. 3 *Duncker* Circulation	Symp. 32 *Diamond* Communities	Symp. 4 *Ziswiler* Morphology	Group 5 *Boswall* Sound records		
18.30–20.00	Pause / break								
20.00	Social Event: Historic Dances						Group 21 *Bock* Morphology		

Programm-Übersicht für Sonnabend, 10. Juni, Saturday, Program overview

Rooms:	A	B	C	D	E	F	G	H	I
7.00– 8.30	Führung durch die Vogelsammlung im Zoo (Einzelheiten siehe Seite 17) Guided tour of the bird collections of the Zoo (for details see page 16)								
7.45– 8.45	Ornithologischer Spaziergang durch den Tiergarten (Einzelheiten siehe Seite 17) Ornithological walk through the "Tiergarten" (for details see page 16)								
9.00–10.00	Plenary *Mayr* Erwin Stresemann								
10.00–10.30	Kaffeepause / coffee break								
10.30–12.30	Filme films			Symp. 6 *King* Ecology	Symp. 20 *Cracraft* Biogeography	Symp. 14 *Zink* Migration	Group 3 *Schmidt-Koenig* Navigation		
12.30–14.00	Mittagspause / break for lunch								
14.00–14.30		Tafelvorträge Poster Sessions							
14.30–18.30 incl. 30 min break	Filme films		Symp. 13 *Wiltschko* Orientation	Symp. 6 – continued –	Symp. 31 *Johnston* House Sparrow	Symp. 35 *Kikkawa* Ecology	Group 20b *Bock* Classification	Group 8 *Duncker* Circulation	Group 17 *Willis* Temperate-tropical
18.30–20.00	Pause / break								
20.00	Filme films		(second IOC)	Standing Committee Seabirds	Standing Committee Nomenclature				

Programm-Übersicht für Sonntag, 11. Juni, Sunday, Program overview

Rooms:	A	B	C	D	E	F	G	H	I
7.45– 8.45	Ornithologischer Spaziergang durch den Tiergarten (Einzelheiten siehe Seite 17) Ornithological walk through the "Tiergarten" (for details see page 16)								
9.00– 9.10	Bekanntmachungen des IOC an alle Mitglieder im **Raum A** Announcement of IOC to all Congress members in **Room A**								
9.10–10.10	Plenary *Perrins* Population								
10.10–10.40	Kaffeepause / coffee break								
10.40–12.40	Filme films		Symp. 33 *Short* South America	Symp. 29 *Gill* Nectar feeding	Symp. 34 *Rautenberg* Tempera-ture	Symp. 24 *Wickler* Pair-bond	Group 7 *Bruns* Ange-wandte Ornith.		(old and new PEC)
12.40–14.00	Mittagspause / break for lunch								
14.00–14.30		Tafel-vorträge Poster Sessions							
14.30–17.00	Filme films	Abbau der Tafeln Removal of Posters					Group 10 *Short* South America	Group 4 *Rautenberg* Tempera-ture	
17.00–20.00	Pause / break								
20.00–24.00	Abschlußabend im Hotel Schweizerhof (nicht in der Kongreßhalle!) Farewell party in the Hotel Schweizerhof (not in the Congress Hall!)								

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